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Stapeliads

of Southern Africa and Madagascar
Volume I



Peter V. Bruyns

2005



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For my family,
Bruce and Steven



New combinations published in this work

Australluma ubomboensis

Duvalia caespitosa subsp. *pubescens*

D. caespitosa subsp. *vestita*

Huernia barbata subsp. *ingeae*

H. blyderiverensis

H. guttata subsp. *reticulata*

H. hislopilii subsp. *cashelensis*

H. hystrix subsp. *parvula*

H. verekeri subsp. *angolensis*

H. verekeri subsp. *pauciflora*

H. zebriana subsp. *insigniflora*

Larryleachia cactiformis var. *feline*

Orbea longii

Pectinaria longipes subsp. *villetii*

Piaranthus cornutus var. *ruschii*

P. geminates subsp. *decorus*

P. geminates subsp. *framsii*

Stapelia grandiflora var. *conformis*

S. hirsute var. *baylissii*

S. hirsuta var. *gariensis*

S. hirsuta var. *tsomoensis*

S. hirsute var. *vetula*

S. paniculata subsp. *kougabergensis*

S. paniculata subsp. *scitula*

Tromotriche pedunculata subsp. *longipes*

Introduction

The stapeliads are the most highly succulent members in the tribe Ceropegieae and belong to the subfamily Asclepiadoideae of the family Apocynaceae. They are all fleshy stem-succulents that are more or less totally without leaves and only rarely have thorns. They exhibit an extraordinarily wide range of flower shapes and sizes (with some of the largest flowers in the plant kingdom found among them) and there is also a wide range of complicated structures in the centre of the flower that are associated with the process of pollination. The flowers are specialized exclusively for fly pollination and this diversity appears to have arisen in response to the wide spectrum of sizes of flies that are present in the region combined with the wide range of geological and topographical niches in the area. These volumes aim to document the extent of this diversity for southern Africa.

The last detailed treatment of the stapeliads was *The Stapelieae* by Alain C. White & Boyd L. Sloane, which appeared in three volumes in 1937. This monograph, with a total of over 1200 pages, covered the whole group in unprecedented detail and today copies are valuable and much sought after. However, much exploration has taken place in the 67 years since *The Stapelieae* appeared. This has led to discovery of many new species and the realization that many of the 'species' discussed by White & Sloane, who never had the opportunity to see any of these plants in their natural habitat, were not species at all. Therefore, despite its pre-eminence, *The Stapelieae* is now considerably out-of-date and is more or less impossible to use for the identification of recent collections. The need for a replacement is consequently quite urgent.

At present the stapeliads consist of, in total, 326 species. These volumes are the first attempt to present a renewed account of them and they deal with the southern African species. For present purposes, southern Africa is taken to be that portion of Africa which lies south of 17°S. Here we include the whole of Namibia, Southern Africa, Botswana and also all of Zimbabwe and Mozambique. The island of Madagascar is (perhaps rather unconventionally) also included, but this is done since the few stapeliads that grow there are more closely related to others in southern Africa rather than to species from further north in Africa.

At present the number of stapeliad species that occur in this area is 182. These 182 species are distributed in 19 genera and all but four of these genera are endemic to the region. Of the 182 species found in southern Africa, all except 15 are endemic to this area and these 15 non-endemic species mostly extend slightly beyond the borders of our area into Angola, Malawi and Zambia. This means that 92% of southern African stapeliads are endemic to the region. Thus these volumes will deal with somewhat more than half of the total number of known stapeliads and will have little overlap with any account of the species from further north.

This work brings together, from many disparate sources, the results of the exploration and research that has taken place over the past 60 years on southern African stapeliads. It consists of two sections, the first of which is introductory and gives the reader some conception of the complexity and diversity that has evolved in the group, especially in the floral structures. There are considerable numbers of terms that are peculiar to the study of asclepiads in the general and stapeliads in particular and these are explained and illustrated with examples in the section on morphology. The second section is the systematic account, which contains details of the individual species. Keys are provided to all the genera, to all the species and to all the subspecies and varieties. All 182 species are described and discussed. Each species is illustrated by means of several color photographs, with a map showing its distribution and with line drawings in which some of the essential, but minute details of the flowers are highlighted. In the photographs, particular emphasis is placed on showing the variability of the species.

Vouchers for the PVB numbers cited in the text are in the herbaria BOL, NBG, PRE, K and MO. Where latitude and longitude 'grid squares' are cited in the text this follows the system of Edwards & Leistner (1971).

Historical Sketch

While there is no doubt that stapeliads have been known in southern Africa for as long as people have been in the area, they were first noticed by Western travelers in 1624 when Justus Huernius found what is today known as *Orbea variegata* on the slopes of Table Mountain. By 1700 *Stapelia hirsuta* was known, and *Quaqua incaenata* and *Q. mammillaris* had also been discovered prior to the publication of Linnaeus's *Species Plantarum* in 1753, although Linnaeus listed only *Stapelia variegata* and *S. hirsuta* in this account. At this stage exploration of the then relatively unknown interior of southern Africa was very tentative and fraught with all manner of dangers, both real and imagined, and this considerably hampered botanical discovery in the region. The documentation of stapeliads of southern Africa can really be said to have begun in earnest with the explorations of C.P. Thunberg and Francis Masson. Thunberg spent nearly three years at the Cape and during this time he and Masson explored some areas together. Masson spent a total of about 12 years at the Cape during two visits to the colony and left for the last time early in 1795. He was sent to the Cape by the king of England, who acted on the advice of Joseph Banks. Banks had been on the first voyage around the world led by Captain Cook and, when the ship put in briefly at the Cape, had been very much impressed by the richness of the flora there. During his two sojourns at the Cape, Masson introduced many novel and remarkable species to Europe, has he send both live plants and seeds back to London. He seems to have had a particular predilection for stapeliads and described 41 species in his book *Stapeliae Novae*, of which most were new in the sense of the time. He cultivated these plants in his garden at Cape Town and took several of them back to London with him, thereby introducing them into cultivation in Europe.

It was around this time (in the latter half of the 18th century) that stapeliads first began to be discovered in other arid parts of the so-called Old World. Pehr Forsskal collected five stapeliads in the Arabian Peninsula during an ill-fated journey in about 1762. Species became known from India in about 1790 when William Roxburgh first documented *Caralluma adscen-ciens*, while Henrietta Antonia Clive collected *C. umbellata* around the turn of the century. It appeared, therefore, to the botanical community of Europe that stapeliads were very exotic and naturally occurred only in hot, arid, far-off lands, where much danger and mystery surrounded them. Consequently, the discovery of similar peculiar plants on the southern shores of Europe itself by Giovanni Gussone in 1828 caused considerable surprise in certain circles. Gussone collected what later came to be known as *Caralluma europaea*, although the Danish botanist and traveler Peder K.A. Schoesboe had been the first to notice it in Morocco



Fig. 1. Neville S. Pillans (courtesy University of Cape Town)

between 1791 and 1793, and it was first detected on the European mainland (in southern Spain) before 1822 by Mariano Lagasca y Seguro (Bruyns 1987b).

Stapeliads continued to be discovered intermittently in southern Africa after the departure of Masson. However, it was the enthusiastic encouragement and enquiries of N.E. Brown at Kew that really stimulated further interest in them at the Cape Colony. Brown worked as a botanist at Kew from 1873 until his retirement in 1914 (after which he continued there unofficially until his death in 1934) and he was particularly interested in succulents, especially the succulent Aizoaceae and stapeliads. An unusual trait for a botanist was that he cultivated many of them personally. This enabled him to gain a greater understanding of them and he also observed and illustrated their flowers in minute detail under the microscope, producing a great many very accurate and extremely attractive drawings. At Brown's instigation, considerable numbers of stapeliads were sent back to Britain by Henry Barkly during the period 1870-7, while he was governor at the Cape. With much new exploration coming alongside the discovery of diamonds deep in the interior of South Africa, more stapeliads were collected well away from Cape Town than had been the case before. Barkly seems to have collected relatively few of these himself, but he certainly encouraged travelers who noticed them to bring him material. He was able to amass an impressive collection of them and these were

described in detail by Brown in his *Stapeliae Barklyanae* (Brown 1890).

During his preparation of the accounts of the *Asclepiadaceae* for the *Flora Capensis* (Brown 1907-09), Brown also encouraged Charles Eustace Pillans, who was a distinguished civil servant in the government of the time in South Africa and his son Neville Stuart Pillans (fig. 1), a botanist employed at the Bolus Herbarium in Cape Town, to gather material. This they did with tremendous success and Brown ended up naming eight species in their honor, one in nearly every genus of southern African stapeliads. They appear to have travelled by rail and stopped at some of the small sidings of the Karoo to make extensive collections around them, presumably residing in the area for a few days. In this way they covered extensive parts of the Great Karoo. In 1926, N.S. Pillans also made an important pioneering journey, part of it by ox-wagon, to the Richtersveld and on this occasion several species were discovered, among which was the singular and rare *Stapeliopsis neronis*. To a large extent they completed the basic exploration for stapeliads of the Cape Province and it could be claimed that only sporadic and relatively minor discoveries have been made since then.

It was shortly after N.E. Brown's death in 1934 that *The Stapeliae* appeared (White & Sloane 1937), the monumental and now famous publication of Alain Campbell White (1880-1951) and Boyd Lincoln Sloane (1886-1955). White was a wealthy person by inheritance (his father having made his fortune in New York real estate), educated in languages, who entertained a lasting passion for chess and, later on, also for certain succulents. Sloane, who was a teacher and principal of various middle schools, mainly in California, was greatly interested in cacti and succulents and had a long-time involvement with the American Cactus and Succulent Society, which included being president of the society in 1931 and 1932 (Mitich 1994). They first met in December 1930 and, after White moved to Pasadena, California, in 1931, he built up a very large private collection of stapeliads. Soon they decided to collaborate on a book stapeliads and this was published at White's expense in September 1933 (White & Sloane 1933). Their first effort was so well received that White decided to expand it to a comprehensive monographic treatment and this appeared in three volumes in February of 1937, again produced at his own expense. After this, together with the South African botanist R.A. Dyer, they produced two volumes on the southern African representatives of the Succulent *Euphorbiaceae* (White *et al.* 1941). Further volumes as sequels to these two were planned, but White had already moved away from California in 1937 and never completed them (Sloane 1952).

Subsequent to the efforts of Pillans, it was

particularly the collecting forays into Namaqualand and the Karoo by Charles Theodore de Mornet Villet and his wife, Elizabeth, that resulted in the discovery of several new species between 1928 and about 1940. Other species became known as new roads gave collectors greater access to previously impenetrable mountainous areas. Many of these were brought to Carl August Lückhoff (fig. 2), who was a medical practitioner and, for a long time, the chief medical officer for the South African Life Insurance Company. He was impenetrably interested in stapeliads at one stage and described several new species. He also published *The Stapelieae of Southern Africa* (Lückhoff 1952) which, although it had only the briefest of texts, provided him with an opportunity to publish many of his remarkable black and white photographs. The collecting activities between 1929 and 1956 of A.G.J. (Hans Herre, who was really most interested in the succulent Aizoaceae and explored extensively in the less accessible parts of the Richtersveld, brought to light some new species, these were grown at the Stellenbosch University Gardens and described by G.C. Nel, a botanist at the university, whose interests also lay more in the direction of the succulent Aizoaceae.

Poth Pillans and Lückhoff lost interest in stapeliads later in their lives and it was only with the curatorship of M. Bruce Bayer at the Karoo Botanic Garden in Worcester, from 1969 until 1987, that interest came to be focused on them once more. A programme of field exploration was undertaken and, for the first time, populations were sampled extensively so that variation within populations rather than just single plants could be observed. For the first time pollination and hybridization experiments were carried out and a comprehensive herbarium record was initiated. L.C. Leach (see below), who had already embarked upon a study of southern African stapeliads in preparation for an account for the *Flora of Southern Africa* project, also came to work at the Karoo Botanic Garden. He stayed in this ideal environment from 1982 until 1990, greatly benefiting from the extensive collections of stapeliads that had been built up there.

Stapeliads were collected in Namibia as early as 1878 by T.J.G. Eén. Systematic exploration of the Namibian flora was begun by Moritz Kurt Dinter, who was a horticulturist and botanist by training. At first he botanised alone and later often in the company of his wife, Jutta Dinter first arrived in Namibia in 1897 and left it for the last time in March 1935. He was especially interested in succulents and he expended much time and effort exploring the arid south of the country where succulents are most common. He came across many stapeliads during the course of these travels.

From 1900 until 1914 Dinter was employed by the German Colonial Government to document the vegetation of Namibia and investigate certain problems that arose in the rural areas. During this period he often had at his disposal a railway carriage which would be parked at a siding to enable him to botanise in the area. He covered much of the less accessible territory, such as the Namib Desert south of Lüderitz and the Great Karas Mountains, by foot or accompanied by an ox-wagon. It is only in areas that Dinter never visited, for example, the Tiras Mountains, the Kaokoveld and the region east of Grootfontein, that any previously unrecorded stapeliads have been found since his time. Thus, for example, the extensive collecting done by Giess, Merxmüller, Volk and Bleissner during the period 1956-68, prior to the publication of *Prodromus einer Flora von Südwestafrika*, revealed almost no new taxa of stapeliads. A few species not known to Dinter were located by Ernst Julius Rusch and his son Ernst Franz Theodor Rusch. Both were farmers and businessmen who lived on the farm Lichtenstein just south of Windhoek. They explored widely in the remote mountains of southern Namibia.



Fig. 2. Carl A. Lückhoff as a medical student in about 1934. (courtesy Marga Hoffmeyr).

In areas outside South Africa and Namibia stapeliads are generally rarer and consequently there have seldom been collectors or botanists who have specialised in their study. In Zimbabwe they appeared very sporadically among the collections of botanists and others. This changed once the amateur botanist Leslie Charles (Larry) Leach (1909-96) gave up his business activities to devote all his time to taxonomic studies of stapeliads, succulent *Euphorbiaceae* and *Aloe*. Leach had been in the army in Britain, the land of his birth, and after encountering problems there he emigrated to what later became Zimbabwe. There he set up a business supplying electrical equipment, especially batteries for vehicles. His business was successful enough for him to sell it off and 'retire' at the age of nearly 50. This gave him more time to pursue his programme of collecting and documenting the stapeliads and other succulents (mainly *Euphorbia* and *Aloe*) in Zimbabwe and other parts of south tropical Africa. He had begun these studies in 1950 and continued them in Zimbabwe until he emigrated to South Africa in 1982. This research resulted in the publication of many papers on their taxonomy and culminated in his revision of *Stapelia* and *Huernia* (Leach 1985; 1988).

In Moçambique, where stapeliads are comparatively rare, the only person who seems to have taken a particular interest in them was the Portuguese agriculturalist Antonio de Figueiredo Gomes e Sousa. He first saw stapeliads during a brief visit, in January and February of 1930, to the arid and desolate Namibe (Mocamedes) district in southern Angola and was very enthusiastic when he found several later that year in the Lebombo Mountains in Moçambique, a country where stapeliads were virtually unknown. His interest in them continued until 1947 and he wrote three accounts of the stapeliads of Moçambique (Gomes e Sousa 1935; 1936; and the final one with Esteves de Sousa in 1947).

The natural history of Madagascar already began to receive attention before 1658 (Reynolds 1966). However, the southern parts of the island, which are home to most of its succulent species, including the stapeliads, were somewhat less accessible and so it was only in 1918 that a stapeliad was first collected. This was found by Raymond Decary and he discovered a total of three species between 1918 and 1932. The later exploration of the even more arid south-western corner of the island led to further species being discovered by Montagnac and others.

In general, for individuals who have discovered species, biographical information is given here only where no information is present in Gunn & Codd (1981). For further information the reader is referred to their book.

Classification of the Stapeliads

The stapeliads belong to the family Apocynaceae, which is the seventh largest family of angiosperms and contains about 424 genera and some 4200 species.

When Linnaeus published his *Species Plantarum* of 1753, the species of Asclepiadaceae and Apocynaceae were placed together in the large grouping which he termed '*Pentandria Digynia*'. This contained all those plants where each flower had five anthers and two ovaries. In 1789 Antoine Laurent de Jussieu, who was one of the main proponents of Linnaeus's 'natural' system of classification, took it a step further and placed all of them in a 'family' (actually he called it an '*Ordo*') which he called the Apocinae. This was named after the genus *Apocynum*, with which many of the species had at one time or another been associated. In 1810 Robert Brown proposed that those genera in which the pollen was attached to 'translators' should be excised from the Apocynoideae and placed in a new family, the *Asclepiadeae* (Brown 1810). This is was generally accepted and, since 1810, these two groups were mostly treated most as separate families.

Over the past three decades evidence has been accumulating from ever more

detailed and careful morphological studies over a steadily increasing range of taxa and from new molecular techniques by means of which parts of the DNA of plants are analysed and compared. It indicates that the generally more derived Asclepiadaceae has arisen within the Apocynoideae (e.g. Sennblad & Bremer 1996). Several studies in which morphological and molecular data have been analyzed together (e.g. Civeyrel *et al.* 1998; Sennblad *et al.* 1998) have shown that only a united Apocynaceae and Asclepiadaceae form a phylogenetically acceptable 'monophyletic' unit. Consequently, just under 200 years after Brown's important paper, it was proposed that the Apocynoideae and the Asclepiadoideae be united once more under a single family, the Apocynaceae (Endress & Bruyns 2000). The organization within this family is shown in Table 1. In this new arrangement most genera of the former Asclepiadaceae are placed within the subfamily Asclepiadoideae. The Asclepiadoideae, commonly, (though rather imprecisely) known as 'milkweeds', includes some 2 700 species which are spread over 222 genera. Representatives of the Asclepiadoideae are most common in tropical to subtropical

areas and they become progressively rarer as one moves away from these warmer part to temperate regions. Most of them are herbs or climbers (trees are rare) and several of them have a weedy or ruderal nature as is well known in the now almost cosmopolitan *Araja sericifera*, *Asclepias curassavica* and *Gomphocarpa fruticosus*. The subfamily Asclepiadoideae is divided into four tribes Asclepiadeae, Ceropegieae, Fockeeae and Marsdenieae. The Fockeeae is sister to the other tree tribes, the Marsdenieae and Ceropegieae are sisters to each other and together are sister to a Asclepiadeae.

The present account deals with the group of asclepiads know as to stapeliads and, in the past, often referred to collectively as the Stapelieae. Traditionally the tribe Stapelieae contained only the highly succulent, practically leafless asclepiads with angled stem (Brown 1902-03; 1907 09; White & Sloane 1937) which, from the time of Linnaeus (1753) up to that of Robert Brown (1810), were all placed in the genus *Stapelia*. Closely related, less succulent taxa without angled stems were referred to the tribe Ceropegieae (Brown 1902-03; 1907-09). However, Hooker (1885), who dealt with the

Table 1. The subfamilies and tribes of the Apocynoideae (after Endress & Bruyns 2000)

Subfamily	Tribe	Number of genera	Distribution	Comment
Rauvolfioideae	Alstonieae	9	Old & New World, tropical to subtropical	
	Vinceae	8	Old & New World, tropical to temperate	
	Willughbeeae	18	Old & New World, tropical	
	Tabernaemontaneae	19	Old & New World, tropical	
	Melodineae	8	Old & New World, tropical to rarely subtropical	
	Hunterieae	3	Old World, tropical	
	Plumerieae	10	Old & New World, tropical to subtropical	
Apocynoideae	Carisseae	2	Old World, tropical to temperate	
	Aiyxieae	7	Pacific Basin, Asia (1 genus in New World), tropical	
	Wrightieae	7	Old & New World, tropical to temperate	
	Malouetieae	12	Old World (1 genus in New World), tropical to subtropical	
	Apocyneae	27	Old & New World, tropical to temperate	
	Mesechiteae	9	New World, tropical to subtropical	
	Echiteae	22	Old & New World, tropical	
Periplocoideae		40	Old World, tropical to arid temperate	
Secamonoideae		9	Old World, tropical to temperate	
Asclepiadoideae	Marsdenieae	29	Old & New World, mainly tropical to subtropical	
	Ceropegieae	46	Old World, tropical to warm temperate	includes the stapeliads, Ceropegia
	Asclepiadeae	145	Old & New World, tropical to temperate	
	Fockeeae	2	Old World, tropical to warm temperate	

Classification of the Stapeliads

genera *Caralluma* and *Frerea* among the *Stapeliaceae* s. str. in the regional that was then known as British India, placed them with others in the *Ceropegieae* and recognized only one tribe for all of them. This arrangement is followed today, with the two tribes united under an expanded *Ceropegieae*. This expanded tribe was known as the *Stapeliaceae* (Bruyns & Forster 1991) until the recent discovery by James Reveal that *Ceropegieae* was actually an earlier name. The *Ceropegieae* in this sense is characterized by horizontal to erect pollinia, each with an insertion-crest along the outer edge or near the apex. This insertion-crest is responsible both for holding the pollinium in the guide-rail and for providing an exit for the pollen tubes from the pollinium (see below for further explanation). The more or less quadrate anthers are generally without any sterile apical appendages (and lack a horizontal slit at the base of the appendage in the few cases where it is present) and in almost a species the sap is clear.

Relationships among the genera

White & Sloane (1937) recognized 18 genera in *The Stapeliaceae*. Several new genera have been described since then, both from southern Africa and north-eastern Africa, and in a recent phylogenetic treatment using morphological characters (Bruyns 2000a) 24 genera were recognized. In this proposed phylogeny (fig. 3) the monotypic *Frerea* from India is the sister to all other stapeliads. *Caralluma*, *Echidnopsis*, *Quaqua* and *Rhytidocaulon*, in which the flowers are generally small and borne in the numerous inflorescences near the apex of the stems, in turn are sisters to the remainder of the stapeliads. Some of these (e.g. *Caralluma*, *Echidnopsis* and *Rhytidocaulon*) are found in north-eastern Africa while *Quaqua* is endemic to southern Africa. The remaining genera are also shared between north-eastern Africa and southern Africa, with more of them in the south. In these the flowers are produced mainly towards the base of the stems and are often considerably larger than in genera such as *Caralluma*. With the description of *Baynesia* from northern Namibia (Bruyns 2000c) and *Ballyanthus* from north-eastern Africa (Bruyns 2001), the number of genera increased to 26. Many of the stapeliads genera have been shown to be monophyletic entities by means of cladistic analyses of morphological characters (Bruyns 1999a, 1999b, 1999d, 1999e, 2002). Nevertheless, the statistical support for the monophyly of several of the genera and the proposed relationships between them is not strong, as is often the case for purely morphological treatments in which the number of characters used is often not much greater than the number of taxa involved. Therefore data sets derived from molecular techniques have been employed to try to produce more robust hypotheses. The

first of these was Meve & Liede (2002), in which 80 species were analysed. These authors recognized 34 genera of stapeliads. Here it was found that the stapeliads still form a monophyletic group. However, support for most of the arrangements within this group was very weak,

with the relationships between the genera, in particular, remaining largely unresolved. Some very weak arguments were advanced for splitting *Caralluma* into seven distinct genera, for maintaining *Orbea* as distinct from *Orbea* and for placing *Ballyanthus* back in *Orbea*

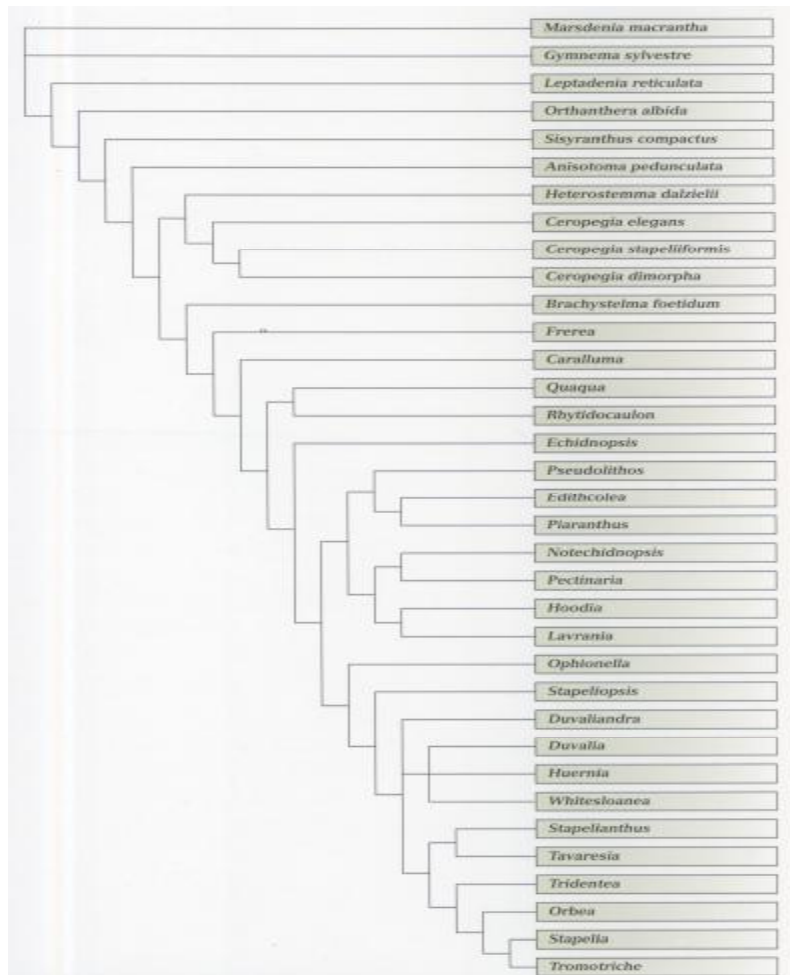


Fig. 3. Simplified cladogram derived from morphological characters showing the possible evolutionary relationship between the genera of stapeliads (from Bruyns 2000a)

Classification of the Stapeliads

Table 2. The number of species in the 31 genera of stapeliads in the various broadly defined regions in which they occur.

Genus	Number of species in White & Sloane (1937)	Total number of species	Species in Southern Centre	Species in North-eastern Centre	Species in Madagascar	Species in India, Myanmar and Nepal	Reference
<i>Anomalluma</i> Plowes	—	2	—	2	—	—	—
<i>Australuma</i> Plowes	—	2	2	—	—	—	this work
<i>Ballyanthus</i> Bruyns	—	1	—	1	—	—	Bruyns 2002
<i>Baynesia</i> Bruyns	—	1	1	—	—	—	Bruyns 2000c
<i>Caralluma</i> R. Br.	112	47	—	33	—	14	Gilbert 1990
<i>Diplocyathia</i> N.E. Br.	1	—	—	—	—	—	—
<i>Drakebrockmania</i> A.C. White & B. Sloane	1	—	—	—	—	—	—
<i>Duvalla</i> Haw.	15	14	10	4	—	—	Meve 1997; this work
<i>Duvallinda</i> M.G. Gilbert	—	1	—	1	—	—	Gilbert 1980
<i>Echidnopsis</i> Hook. f.	9	21	—	21	—	—	Bruyns 1988; Lavranos 1993; Thulin & Hjertson 1995
<i>Edithcolea</i> N.E. Br.	2	1	—	1	—	—	Lavranos 1970
<i>Frerea</i> Dalz.	1	1	—	—	—	1	Tetali et al. 1997
<i>Hoodia</i> Sweet ex Decne.	16	14	13 ^a	—	—	—	Bruyns 1993
<i>Hoodopsis</i> C.A. Lückhoff	1	—	—	—	—	—	—
<i>Haernia</i> R. Br.	49	49	33	14	—	—	Leach 1988; this work
<i>Huernicopsis</i> N.E. Br.	4	—	—	—	—	—	—
<i>Larryleachia</i> Plowes	—	5	5	—	—	—	—
<i>Lavrania</i> Plowes	—	1	1	—	—	—	Plowes 1985
<i>Notechidnopsis</i> Luvr. & Bleck	—	1	1	—	—	—	Bruyns 1999d
<i>Ophioneila</i> Bruyns	—	2	2	—	—	—	Bruyns 1999e
<i>Orbea</i> Haw.	—	56	30	27	—	—	Bruyns 2002
<i>Pectinaria</i> Haw.	6	3	3	—	—	—	Bruyns 1981a
<i>Paranthus</i> R. Br.	16	7	7	—	—	—	Meve 1994; this work
<i>Pseudolithos</i> P.R.O. Bally	—	4	—	4	—	—	Bruyns 1990c; Meve & Liede 2002
<i>Quaqua</i> N.E. Br.	—	19	19	—	—	—	Bruyns 1999a
<i>Rhytidocaulon</i> P.R.O. Bally	—	11	—	10	—	—	Bruyns 1999g; Hanáček & Růžek 2000; Lavranos & Mies 2001b
<i>Richtersveldia</i> Meve & Liede	—	1	1	—	—	—	—
<i>Socotrella</i> Bruyns	—	1	—	1	—	—	Bruyns & Müller 2002
<i>Stapelia</i> L.	100	29	28	—	—	—	Leach 1985; this work
<i>Stapelanthus</i> Choux	2	6	—	—	6	—	Bruyns & Klak 2004
<i>Stapelopsis</i> Pillans	1	8	8	—	—	—	Bruyns 1981a
<i>Tavaresia</i> Welw.	3	2	1	—	—	—	Leach 1974b
<i>Trichocaulon</i> N.E. Br.	27	—	—	—	—	—	—
<i>Tridentea</i> Haw.	—	8	8	—	—	—	Leach 1980a; Bruyns 1995a
<i>Tromotriche</i> Haw.	—	9	9	—	—	—	Leach 1984b; Bruyns 1995a
<i>Whiteskaneia</i> Chiov.	—	1	—	1	—	—	Bally et al. 1975; Bruyns 1998b
Total species	367	328	182	120	6	15	—

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(despite the fact that their results showed that it was nested within *Duvalia*, so that it should, if anything, be sunk into *Duvalia*!).

A further and more extensive molecular treatment has been embarked upon at the University of Cape Town (Nowell *et al.*, unpublished), in which 165 species were analysed. More detailed studies have been carried out at the level of species for *Stapelanthus* (Bruyns & Klak 2004) and for *Stapeliopsis* (Bruyns *et al.* 2005). The generic limits within *Caralluma* are also in the process of being investigated. The genera recognized at present are listed in table 2.

In Meve & Liede (2002) perhaps the most significant result is there is large assemblage of species (all of which occur in north-eastern Africa and further east) belonging to the genera *Caralluma*, *Echidnopsis* and *Rhytidocaulon* that are sister to all other stapeliads (as in the morphological treatment). In the branch that is sister to the former genera there is a well-supported branch consisting of *Whitesloanea* and (in our own analyses) the two Socotran endemic genera *Duvaliandra* and *Socotrella*. These East African taxa in turn are sister to the remainder of the stapeliads. This remainder contains the vast majority of species, including all of the southern African stapeliads. These arrangements reinforce the hypothesis (vaguely expressed in Meve (1997) but cladistically investigated in Bruyns (2000b)) that the stapeliads originated in north-eastern Africa and later migrated into southern Africa. The presence of East African taxa within this southern clad is as yet insufficiently explored. Our own investigations suggest that within *Huernia* and *Orbea* there has been dispersal from the southern African region back into north-eastern Africa. These are summarized in fig. 4.

Species concepts among the Stapeliads

As in most succulent plants, the 'folk concept' of species (Cronquist 1988), in which groups are formed intuitively from 'essentially similar' individuals and termed species, has largely held sway among the stapeliads. Where only small amounts of material were available, this has led to the recognition of many unnatural taxa and the almost total exclusion of the concept of variation within taxa. Early collectors such as Masson at the Cape and Jacquin in Vienna, rarely had more than one plant on which to base their knowledge and consequently the 'species' that they described often bore little relationship to the position in nature. Brown (1890) came to appreciate the variability of some taxa and consequently many of his 'species' are recognized as such today, though others, where he saw less material, have not stood the best of time.

Among the succulent Aizoaceae, recent revisions have shown that there are frequently as many as five times (and up to 20 times) as many names as species (Ihlenfeldt & Gerbaulet 1990; Hammer 1993; Klak & hinder 1998). L.C. Leach found that certain species of stapeliad also have large numbers of synonyms but that this what not generally such a problem among the stapeliads. Nevertheless, it is a puzzling fact that, in all the revisions and taxonomic work of Leach, there is no articulation of a species concept and, generally, he seems to have used little more than the existence of differences to define species, i.e. nothing more than the 'folk

concept' mentioned above. Where he saw little material, this led him to describe too many taxa and his classifications then turn out to have little predictive value.

There is a fast literature on the subject of what constitutes a species (Luckow 1995). Many botanists seem to accept the principle that persistent discontinuities must be present in at least two 'good' characters to define species (e.g. Stebbins 1950; Hedberg 1957; Wiley 1981; Sidwell 1999). A 'good' character is taken to be one which is readily observed (i.e. usually a morphological character for which a magnification of x10 is enough) and

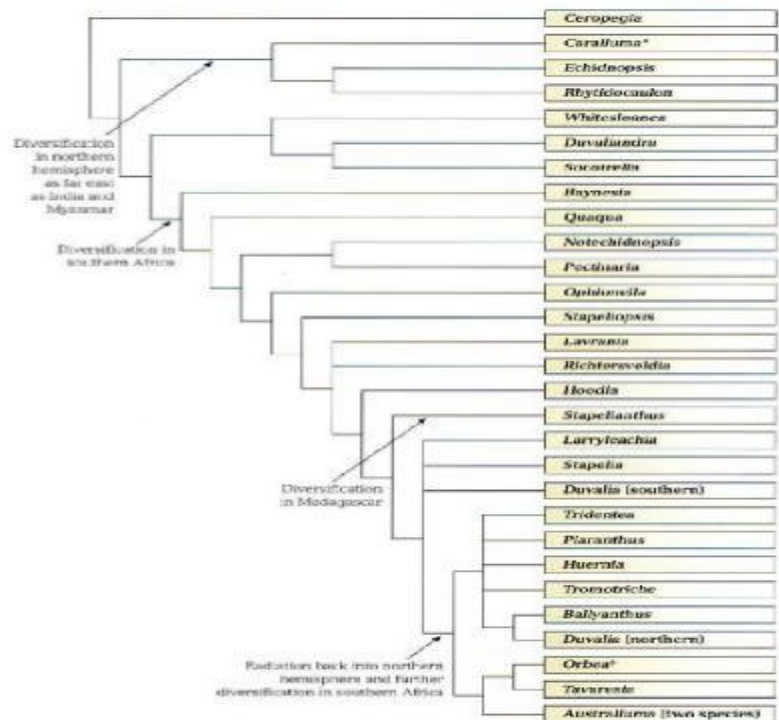


Fig. 4. Simplified cladogram showing possible relationships among the genera of the stapeliads based on unpublished molecular data. * Including *Edithcolea*, *Frerea* and *Pseudolithos*. + Including *Angolluma*, *Orbeanthus*, *Orbeopsis* and *Pachycymbium* but excluding *O. umbonensis*, which is included in *Australium*.

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where variation can be assessed by measuring or counting. It is considered that these discontinuities are largely brought about by reproductive isolation, since interbreeding would normally lead to a 'watering down' of these differences. This is generally how species are defined here. Nevertheless, there are a few exceptions. In a few cases taxa separated by consistent differences in only one character have been found to co-exist but maintain their distinctness. Consequently here, once again, reproductive isolation is present and these are recognised as distinct species. A particular problem is presented by taxa which are spatially distinct but which differ only marginally in morphological features, e.g. the pair of species *Huernia nouhuysii* and *H. thuretii* or the pair *H. guttata* and *H. transvaalensis*. Some authors

have taken the view that such taxa could interbreed if they co-existed and so should belong to the same species (Mayr 1964, but see Cracraft 1992 for a very different view). Several such cases maintained as distinct species by Leach (1985; 1988) have been placed under single species here, usually as subspecies but sometimes without any taxonomic rank (see *Huernia barbata*, for example). In the past there has been a relatively inconsistent approach to the allocation of the ranks of subspecies and variety in the stapeliads. For example, it was demonstrated that all the features separating *Huernia zebrina* subsp. *zebrina* from subsp. *magniflora* were subject to such variation that plants could be placed in the correct subspecies only by their

place of origin (Leach 1988) so that there were characters at all which separated these two subspecies. One the other hand, as discussed below, *H. hystrix* subsp. *parvula* is separated by a consistent and reliable difference in the shape of the inner corona lobes and by several other less reliable features, and this taxon was previously recognised only at varietal level. A similar situation exists in *Orbea gerstneri* where traditionally two subspecies have been maintained which differ markedly (Leach 1978a). In general in this account the rank of subspecies is applied where two geographically complementary taxa occur which differ in only one 'reasonably reliable' character. The rank of variety is only rarely used: where taxa that occur together differ in a single character, and where many intermediates are often found.



Fig. 5. *Caralluma priogonium*, an example of a possibly 'ancestral' stapeliad with ± 30 mm thick succulent stem which taper into slender, ephemeral inflorescences which may be up to 1 m long, here bearing flowers and fruit, PVP 8677, Pangani River, Tanzania.

Morphology of the Stapeliads

The stapeliads are highly succulent plants. Succulents are very plentiful among the stapeliads and are not by any means restricted to the stapeliads, with probably nearly 800 species out of the total exhibiting some form of succulence. However, succulent asclepiads are nearly totally restricted to the Old World and, although the family is well represented in the New World (i.e. in the Americas), hardly any succulent taxa occur there (although see Goyder & Morillo 1994 for an exception). The number of succulents is much lower in the other subfamilies of the Apocynaceae, with a total of at most 30 species in the two genera *Adenium* and *Pachypodium*.

Asclepiadaceous succulents are of several types.

(1) Leaf-succulents

These are comparatively rare among the asclepiads and are more or less confined to the genera *Dischidia* and *Hoya* and a few related minor genera. Most of these are climbers, epiphytes or lithophytes, and they hail exclusively from the eastern perimeter of the Indian Ocean from India eastwards and southwards to Australia. There are particularly large numbers of species in the rainforests of Indonesia, Malaysia and Papua New Guinea. Here, on exposed branches, stems and rock surfaces, there is a regular and frequent change from wet to dry conditions which has favored the development of succulence in several families (Von Willert *et al.* 1992: 26).

Some species of *Ceropegia*, particularly Africa, are also left-succulents.

(2) Stem-succulents

Among the asclepiads stem-succulents are essentially of two kinds. In the one the stems are angled, contain clear sap and bear mostly much reduced leaves, these are the so-called stapeliads.



Fig. 6. *Duvalia maculate*, plant with minute stems (often only 10 mm long) forming a dense, tightly packet mat around the base of a shrub, PVP 5737, near Helmeringhausen, Namibia.

In the other the stems are mostly cylindrical (though see *Cynanchum rossii* from Madagascar for an exception with angled stems) and the sap is milky or yellowish. These belong to a different tribe, the Asclepiadeae, and differ significantly florally from the stapeliads. Examples of these are found in the genera *Cynanchum*, *Folotsis* and *Sarcostemma* (sometimes in all included in *Cynanchum*). By far the majority of these are found in Madagascar, with only a few in Africa and elsewhere in the Old World.

There are also many species of *Ceropegia* which exhibit stem-succulence. In this genus the stems are cylindrical and the sap is more or less clear. Such species are found mainly in Africa and parts of Arabia.

(3) Tuberous succulents

Here the underground parts of the stem are much modified into a water-storing tuber, which may be quite massive and rich 1 m in diameter, with more slender, leafy, above-ground stems. Examples of these are furnished by the principally southern African genus *Fockea* and some species of *Ceropegia* which are mainly found in Africa.

Within the Ceropegieae the stapeliads (i.e. the group traditionally known as the Stapelieae) form a substantial part of the tribe, with 31 genera and 328 species. They are the most highly succulent members of the tribe (and the family as a whole) and form a monophyletic group which is united by the derived character of fleshy flowers (Bruyns 2000a). The monotypic genus *Frerea*

practically leafless with angled stems.

While we have therefore characterized stapeliads as stem-succulent asclepiads with clear sap, usually angled stems, mostly very reduced leaves and fleshy flowers, this does not give any idea of the diversity within the group or the complexity of many of the structures on the plants. In addition, succulents often exhibit extreme reduction in many of their vegetative and reproductive organs so that it is not always obvious how the structures seen correspond to those found in other plants. The flowers are especially complicated in the asclepiads and so some effort will be expended explaining the different structures and how they function.

The plant

Amongst the stapeliads the rootstock consists only of roots which are usually slightly succulent and only rarely become slightly hard and fibrous in the species of *Hoodia* and in larger specimens of *Larryleachia*. No underground



Fig. 7. *Stapelianthus montagnacii*. Plant with prostrate stem forming dense mats on floor of forest, PVB 6195, north of Tulea, Madagascar.



Fig. 8. *Orbea maculata* subsp. *maculata*, several pieces removed from habitat, showing the development of underground rhizomes (the white parts, bearing only small tubercles) from which small clusters of stem develop above the surface of the soil, PVB 6986, near Gweta, Botswana.



Fig. 9. Non-rhizomatous stems of *Duvalia caespitosa* subsp. *vestiva*, PVB 6788, Stormsvlei.



Fig. 10. Rhizomatous stems of *Duvalia caespitosa* subsp. *caespitosa*, PVB 7489, Hankey. This and the previous picture show the variability in this character within a single species.

tuber ever develops. Although this was said to be the case in *Frerea* (Sarkaria 1980), none of the many seedlings grown in Cape Town have ever shown any signs of it. The roots vary greatly in thickness. Very fleshy roots up to 5 mm thick are often seen in *Tridentea*, while in *Stapelopsis exasperata* and in many *Stapelianthus* species they are only 0.5 mm thick.

In the closely related genus *Ceropegia* the plant is of very variable size. Many species are slender climber where the stem is of more or less indeterminate length and may reach 10 m or more. There are other species which have largely lost the climbing tendency and form small herbs or highly succulent shrubs but occasionally still produce climbing stems. In yet others there is no tendency to climb and all the stems are of reduced length. In some of these cases the plant consists of a highly succulent shrub in which the stem mainly branch from their bases (e.g. *C. dichotoma* and *C. fusca*, Bruyns 1986b; *C. dimorpha*, Rauh 1961) and these begin to resemble the plant found in the stapeliads.

In contrast to this, within the stapeliads, the climbing habit has been lost entirely and this has been accompanied by a dramatic decrease in the length of the stems. All of them have thick, fleshy, mostly quite soft stems, the length of which is mainly limited to 150 mm or less, although there are a few, such as *Caralluma procumbens* and *Tromotriche baylissii*, where the stems (which are creeping and pendulous respectively) may be up to 3 m long. Woodiness is unknown and only in the larger species of *Caralluma*, *Hoodia*, *Larryleachia* and *Quaqua* do the bases of the stems become somewhat hard and fibrous. In *Hoodia parviflora* the stems may reach 2 m in length; this is the only stapeliad which nearly qualifies as a tree.

By comparison with the plant found in putative ancestors like *Marsdenia* and many *Ceropegia*, it would appear that within the stapeliads the least derived growth form is

an upright, many-stemmed shrub, perhaps rooting only from a single, central stem, like a small trunk, and bearing slender, often somewhat ephemeral inflorescences. This 'ancestral' form is found especially in *Caralluma* (fig. 5) and *Rhytidocaulon*. It has been modified in several directions.

- (1) A tendency for the plant to spread out at ground level from the central stem to form a clump which roots on the side branches. This has developed further along three lines:
 - (a) The stem have become shorter to that plants from dense mats of small stems that are often not more than twice as long as broad. These reach their most extreme form in *Duvalia* (fig.6) and in the southern African genera *Piранthus* and *Pectinaria*, which are particularly noted for their short

stems and their mat-forming habit.

- (b) The stems have retained their length but become wholly prostrate and can form small dense mats or diffuse, spreading carpets with roots present all along the stem. These have developed independently in many instances, e.g. in the genera *Echidnopsis*, *Huernia*, *Ophionella*, *Orbea* and *Stapelianthus*, (fig. 7)
- (c) Plants have developed horizontally spreading, underground rhizomes that may extend for a distance of up to 1 m from the original plant (in *Tromotriche revolute*). Usually the subterranean rhizomes are thin and they are often rounded (i.e. without angles or tubercles) and they become thicker, erect and conspicuously tuberculate on emerging from the soil. This growth form has developed independently



Fig. 11. *Larryleachia picta*, plant reduced to a single larger stem with another smaller stem emerging alongside it, PVB 7565, north of Williston.

in many genera. Apart from a few species of *Caralluma* (for example *C. burchardii*, *C. europaea* and *C. munbyana*) and some species of *Orbea* in Tanzania, Kenya and Ethiopia (Gilbert 1990), it is found mainly in southern Africa. Here, examples occur in both tropical and temperate regions, as in *Duvalia polita*, *Huernia longii*, *Orbea maculata* (fig. 8), *Stapelia engleriana*, *Stapeliopsis exasperata* and *Tromotriche revoluda*. In a few species (especially in *Tromotriche*) this has been modified into long, hanging stems.

- (d) reduction in the number of stems in a clump until it consists of a single, often quite small and short stem. This has happened independently in the genera *Laryleachia* (fig. 11), *Pseudolithos* and *Whitesloanea*, although in the first two genera there is a trend within the genus towards this from and not all species have it.
- (2) A tendency to form large and robust, free-standing shrubs. This habit is found in few species of *Quaqua* (fig. 13). Such plants begin life sheltered by a shrub or stone but

soon outgrow it; in *Hoodia parviflora* the plant may be up to 2 m tall with stems up to 110 mm thick. From their probable ancestors they seem to have retained the trunk-like, central stem which bears roots and generally they do not root naturally on side branches. In *Hoodia* a small taproot may develop which, in the larger species, again suggests in tree-like tendency (Bruyns 1993)

One may observe here that, while stapeliads never become as large as some succulent members of *Euphorbia* or as the larger representatives of the Cactaceae, they actually exhibit a range of growth forms similar to both these groups. In *Euphorbia* one finds solitary-stemmed species (e.g. *E. obesa*) but rhizomatous species are rare (e.g. *E. tridentata*, *E. knuthii* subsp. *knuthii*) and prostrate-stemmed, mat-forming species are also rare (e.g. *E. hepatica*). Large, tree-forming species are common and, unlike the stapeliads, tuberous species are also common. In the Cactaceae all the above growth forms may be observed, as well as tuberous species and even epiphytes.

In all species of stapeliad the leaf-rudiments

is borne on a raised tubercle (or podarium) which is a much swollen leaf-base. In the asclepiads in general the leaf-base swells up between the stipular denticles at the base of the leaf-lamina and the axillary bud which remains right against the stem (Troll 1935-7). This is quite different to the situation in the Cactaceae, where the axillary bud may even lie towards the tip of the tubercle. These tubercles are arranged in rows along the stem and are often physically fused into the rows to form conspicuous wings. This lends the stems their characteristically thick, angled appearance, which is one of the most distinctive features of stapeliads (see fig. 23 A). Among more distantly related genera in the asclepiads such leaf-bearing tubercles are absent and they do not develop significantly in the other stem-succulent group, that is, in *Cynanchum*, *Folotsia* and *Sarcostemma*. However, there is a tendency within closely related *Ceropegia*, as the stems become more succulent, for the petiole to decrease in length and for the leaf to arise on tubercle which is raised out of the stem, exactly as in the stapeliads. These tubercles can become quite prominent in such highly succulent species

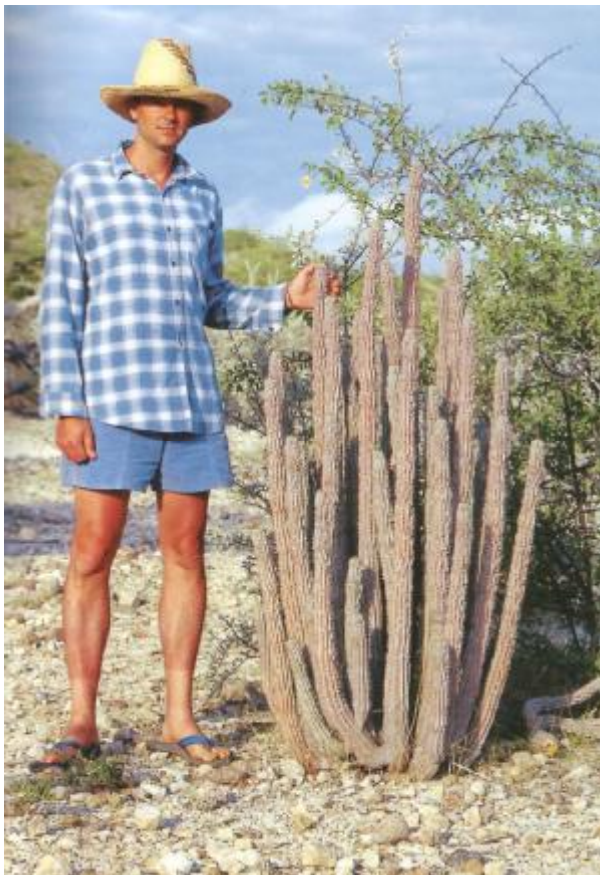


Fig. 12 *Hoodia parviflora*, tall, erect shrub, in this case about 1.5 m tall (a modest specimen), with Stefan Steiner, south of Epupa Falls, Namibia.



Fig. 13. *Quaqua pillansii*, erect shrub about 45 cm tall, PVB 2426, south of Laingsburg.

MORPHOLOGY OF THE STAPELIADS

as *C. dimorpha*, where they project from the stem for up to 10 mm or more but, even in this species and in others with tubercles, the stems remain cylindrical.

In most species of stapeliad there are just four rows of tubercles along the stem, which is then four-angled. In such four-angled stems the leaves are in opposite pairs with each subsequent pair rotated through 90°. This is the same decussate arrangement that is common across the whole family. The base of each tubercle is extended into a ridge which runs downwards to meet the next tubercle lying immediately below it, in the process passing right through one pair of leaves. There is usually a more or less continuous groove running longitudinally down the stems between each pair of adjacent angles.

In *Frerea indica* (fig. 14) these angles are absent. Here the decussately arranged leaves are still borne on distinctly spreading tubercles but the ridge beneath each tubercle runs down only a short way and peters out during the internode in which the tubercle lies, before the next pair below is reached.

It should be noted here that the development of angled stems is not unique to the stapeliads but is also found in stem-succulents in several other families. They are widespread in *Euphorbia* and in the Cactaceae and also occur in the Vitaceae and a few Cucurbitaceae in Madagascar (Troll 1935-7; Rauh 1967). Generally they are associated with a reduction in the surface area of the leaf and the increasing photosynthetic activity of the stem to replace that of the reduced leaves.

As in *Euphorbia* and in the Cactaceae, there are many stapeliads in which the stems have more than four angles and this has evolved

independently in several genera. This change is brought about by the leaves being in whorls rather than in opposite pairs (Troll 1935-7; Bruyns 1988; 1993). The same development takes place in *Ceropegia*, as in *C. stapeliiformis*, where the leaves are produced in whorls of three.

In *Huernia* and *Stapelianthus*, most species have four- or five-angled stems but the number rises to six in a few species increases very much in *H. pillansii* and *S. pilosus*. In *Echidnopsis*, *Notechidnopsis* and *Pectinaria* there are always at least six angles, in *Hoodia* and *Laryleachia* at least 10 and in a few species of *Echidnopsis*, *Hoodia* and *Laryleachia* up to 25 or even more.

One other curious adaptation, which is found only in some of the tropical to subtropical species of *Orbea*, should be mentioned here. In these the tubercles become long and slender and may be several times as long as the stem is thick. In southern Africa this is particularly associated with species that grow among scattered tufts of grass or leaf-litter under trees and it seems to be an attempt to camouflage the plant by breaking up the outline of the stems. A good example is provided by *Orbea longidens* (fig. 15).

In most asclepiads the leaves are prominent and this is true of many species of *Ceropegia*. Within *Ceropegia* there is a noticeable trend for the succulence of the stems to increase and the surface area of the leaves to decrease and, in a few highly succulent species, the leaves are reduced to tiny, caducous, deltoid rudiments (as in *C. stapeliiformis*). This trend, for an increase in the succulence of the stems to go along with a reduction in the size of the leaves, is typical of many families. Generally, as the surface area



Fig. 15. Long tubercles on the stems of *Orbea longidens*, PVB 8531, north of Manhica, Maputo Province, Mozambique.

functions are taken over by the stems.

Among the stapeliads there is only one species [*Frerea indica*] which bears true laminate leaves and these are 1-5 cm long. In all other leaves are reduced to tiny rudiments. In a few genera there is still the trace of a midrib and a minute blade can be made out. This is particularly the case in the northern hemisphere in the genera *Caralluma*, *Echidnopsis* and *Rhytidocaulon* (fig. 16), where the leaf-rudiment has a lanceolate to ovate or cordate shape. These structures are mostly minute but, in exceptional cases, may reach 5 mm diameter, as has been found in *Caralluma umbellata*. In the southern hemisphere the leaves are generally harder to make out (fig. 17) and it is only in *Baynesia*, *Australluma peschii* and *Stapelia* where leaf-rudiments with a somewhat leaf-like shape may be seen. The most extreme case is *S. gettliffei*, where they reach 11 mm in length. Nevertheless, traces of a leaf-like shape can sometimes be found and this has been seen particularly in *Hoodia*, where the spines may be quite leaf-like in young seedlings (Bruyns 1993).

Apart from the general reduction from a laminate leaf, three further specialisations have taken place.

- (1) In the two genera *Hoodia* and *Tavaresia* which are quite distantly related, the leaves have been modified into spines. In young plants the leaves still have a slight midrib and blade so that the spines are clearly modified from such structures. In both cases the epidermal cells of the



Fig. 14. *Frerea indica*, in lush growth with comparatively large leaves and almost cylindrical stems, PVB 5925, Junnar, India.

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spines are long and narrow (fig. 18H), as is the case in the most unspecialized spines in the Cactaceae (Schill *et al.* 1973). Unlike the situation in *Euphorbia*, where spines are derived from several different organs (White *et al.* 1941; Uhlarz 1974a), this is the kind of spine found in the asclepiads.

(2) Reduction of the leaf-rudiment so that no trace of it can be found at the tip of the tubercle. This has happened independently in *Duvaliandra*, *Notechidnopsis*, *Ophionella*, *Pectinaria*, *Pseudolithos*, *Quaqua*, *Stapeliopsis* and *Whitesloanea* and is particularly common in southern African species.

(3) 'Microloma-type' leaflet: in several genera of the Asclepiadoideae (especially, *Emicarpus*, *Eustegia* and *Microloma* in southern Africa) the leaf develops a 'trifoliate' shape with two spreading extensions near the base (Bruyns 1999f; Bruyns & Linder 1991). Although this is known in several species

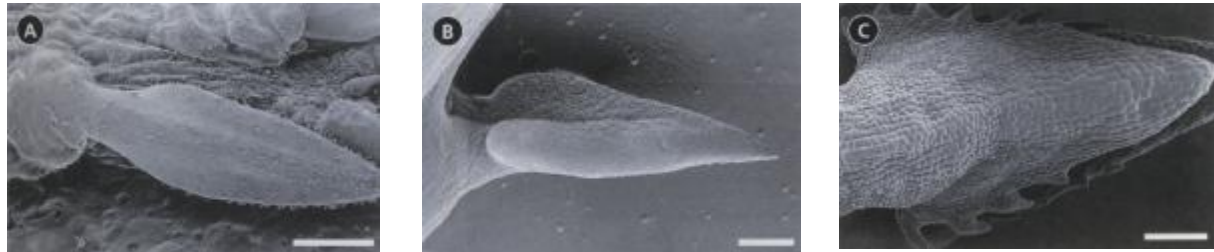


Fig. 16. Leaf-rudiments among northern taxa, with Sem A. *Rhiditocaulon macrolobum* subsp. *macrolobum* (hort.) B. *Caralluma edulis*, Western India (hort.) C. *Caralluma indica*, PVB 5876 D. *Echinops squamulata* (Noltee 1968) E. *Anomalluma dodsoniana* (hort.). Scale bars (approx.): A. 1 mm; B,D. 500 μ m; C,E. 200 μ m

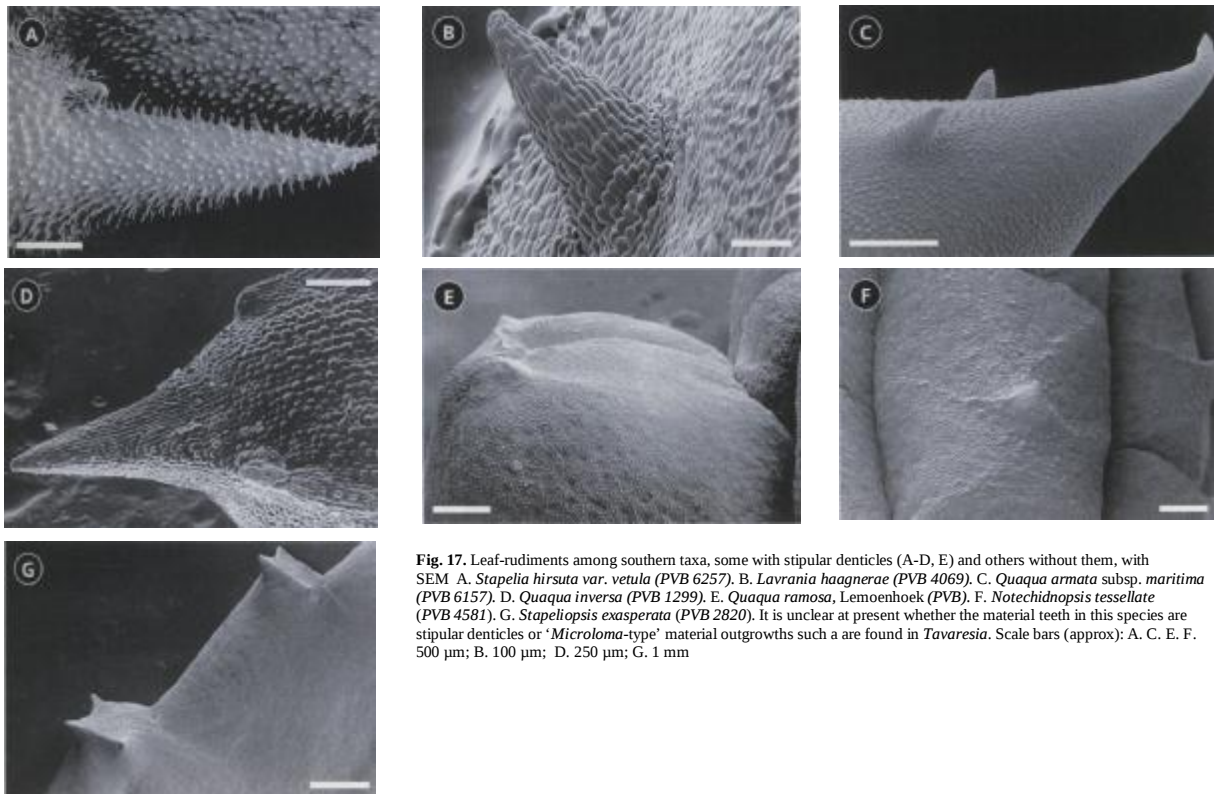


Fig. 17. Leaf-rudiments among southern taxa, some with stipular denticles (A-D, E) and others without them, with SEM A. *Stapelia hirsuta* var. *vetula* (PVB 6257). B. *Lavrania haagnerae* (PVB 4069). C. *Quaqua armata* subsp. *maritima* (PVB 6157). D. *Quaqua inversa* (PVB 1299). E. *Quaqua ramosa*, Lemoenhoek (PVB). F. *Notechidnopsis tessellate* (PVB 4581). G. *Stapeliopsis exasperata* (PVB 2820). It is unclear at present whether the material teeth in this species are stipular denticles or 'Microloma-type' material outgrowths such as are found in *Tavaresia*. Scale bars (approx): A. C. E. F. 500 μ m; B. 100 μ m; D. 250 μ m; G. 1 mm

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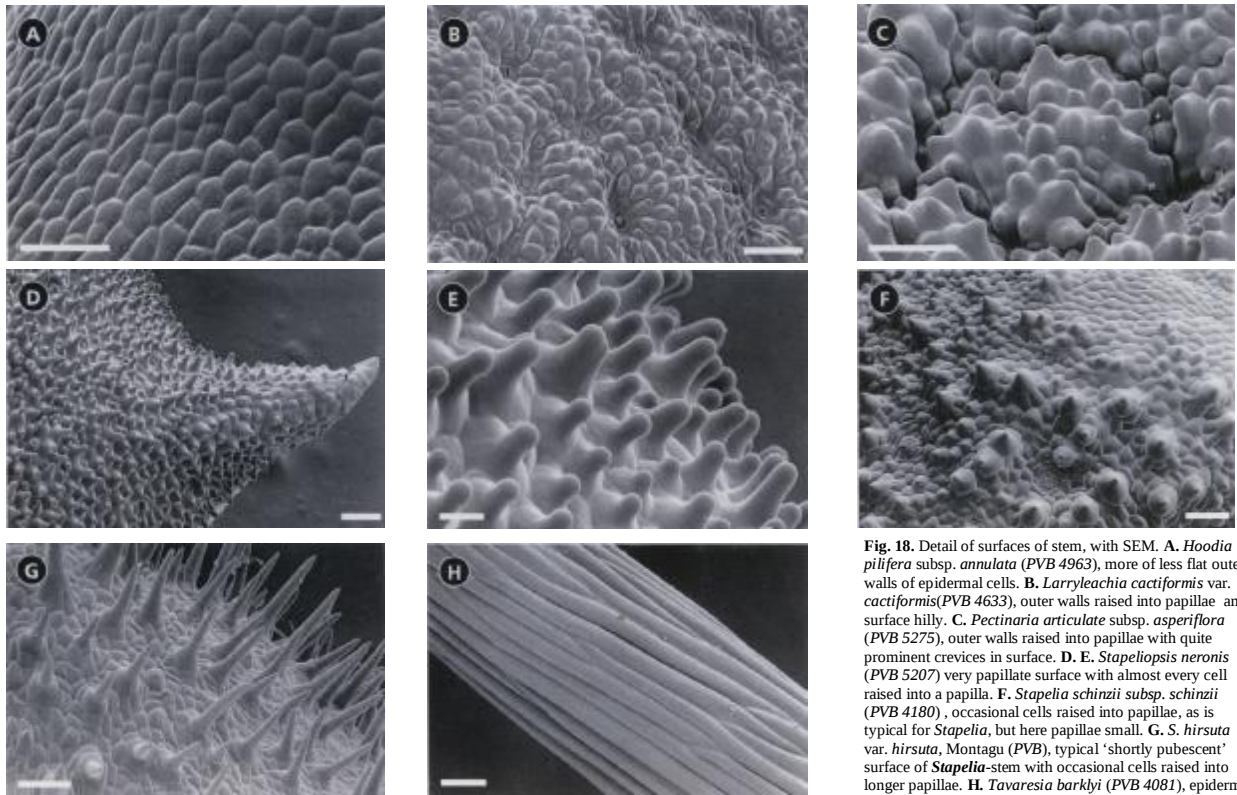


Fig. 18. Detail of surfaces of stem, with SEM. **A.** *Hoodia pilifera* subsp. *annulata* (PVB 4963), more or less flat outer walls of epidermal cells. **B.** *Larryleachia cactiformis* var. *cactiformis* (PVB 4633), outer walls raised into papillae and surface hilly. **C.** *Pectinaria articulate* subsp. *asperiflora* (PVB 5275), outer walls raised into papillae with quite prominent crevices in surface. **D. E.** *Stapeliopsis neronis* (PVB 5207) very papillate surface with almost every cell raised into a papilla. **F.** *Stapelia schinzii* subsp. *schinzii* (PVB 4180), occasional cells raised into papillae, as is typical for *Stapelia*, but here papillae small. **G.** *S. hirsuta* var. *hirsuta*, Montagu (PVB), typical 'shortly pubescent' surface of *Stapelia*-stem with occasional cells raised into longer papillae. **H.** *Tavaresia barklyi* (PVB 4081), epidermal cells on spine. Scale bars (approx.) A-D, F, G, 100µm, E, H, 25 µm.

of *Ceropegia*, it is found in the stapeliads only in *Tavaresia* (Melve & Alberts 1990b) and possibly also in *Stapeliopsis exasperata* (fig. 17 G).

Although it is not obvious to a casual observer, the surface of the stems is covered by a thick wax layer and this, together with relatively low numbers of stomata, is their main defense against evaporation. The surfaces of the stems beneath this wax covering have been examined in many stapeliads in a search for useful characters for their classification and examples are shown in fig. 18. This has shown that, while the stems are frequently covered with hairs in many asclepiads, in the stapeliads such an 'indumentum' is almost universally lacking. Many of them turn out to have a distinctly dull almost smooth surface where the epidermal cells have nearly flat outer walls (fig. 18 A). In others the outer wall of each epidermal cell is raised into a papilla. The surface can be 'hilly' (e.g. *Larryleachia*, fig. 18 B) or regularly rugulose (as in *Baynesia*, *Rhytidocaulon* and *Stapelinthus*) and it is occasionally deeply and irregularly crevassed as in *Pectinaria* (fig. 18 C). In a few genera there are papillae which project to form hair-like strictures and this is especially true of *Rhytidocaulon*, where these 'hairs' are

multicellular, and *Stapelia*, where they are unicellular (fig. 18 F-G). In *Stapelia* each of these 'hairs' is raised up by the surrounding cells onto a slight pedestal, an arrangement also found in *Piранthus* and some species of *Echidnopsis*. The papillae on the stems of *Stapelia* are always present (even in apparently glabrous-stemmed species) and fig. 18 F-G gives some idea of the extent to which they vary in length.

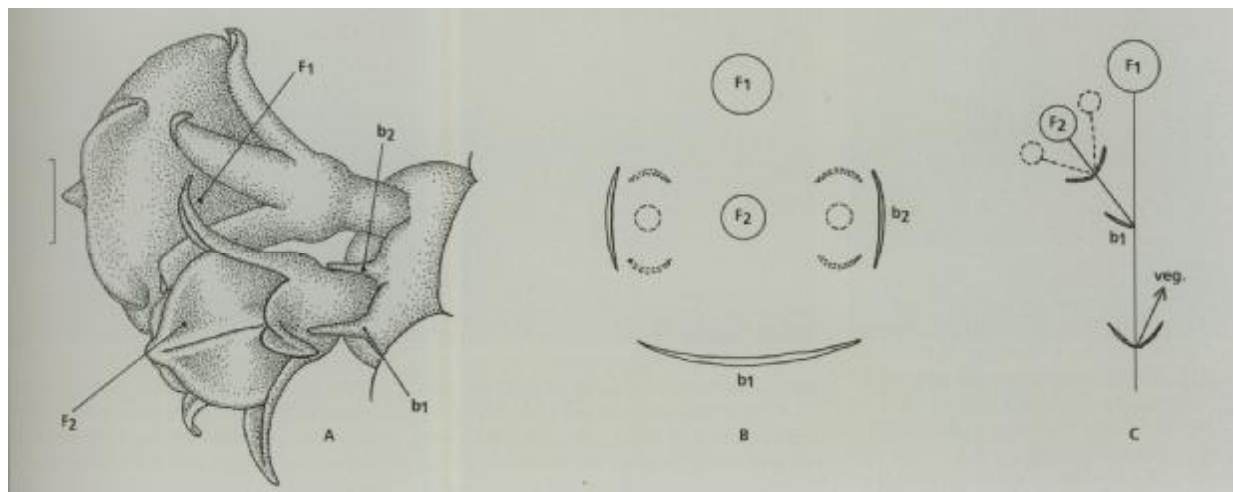
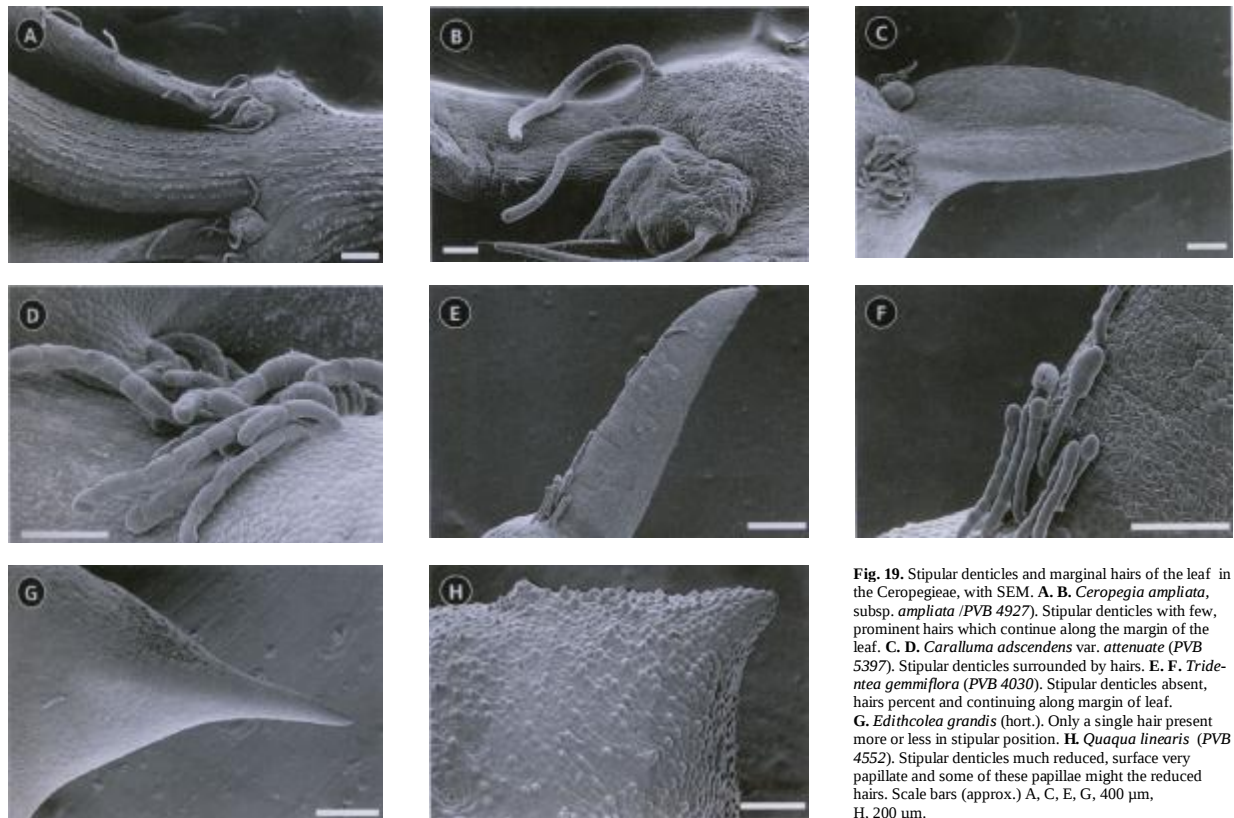
Examination of the stem by means of the SEM has also shown that small stipular denticles are often present (fig. 17) and that in a few cases traces of the hairy 'indumentum' that is common in other stapeliads can be found (fig. 19).

In many asclepiads the flowers are borne in small groups next to the leaf-pairs. This location led to the initial belief that the inflorescences where axillary and that they shifted into an extra-axillary position (Hochstätter 1850), which would have made the flowering stem a monopodial structure. However, it was gradually realized that in the asclepiads the flowering axis is not continuous but is made up of as many branches as there are inflorescences, each branch developing from the previous one. Thus, at each inflorescence the stem is terminated by one of the flowers in the inflorescence

and this would mean that the flowering axis is a closed, determinate sympodium (Demeter 1922; Troll 1959, for *Ceropegia*). In fig. 20 a small inflorescence in *Echidnopsis scutellata* is shown and in fig. 20 C the growth pattern of the stem around this inflorescence is indicated to show how the inflorescence comes to take up an apparently axillary position.

In the stapeliads the fact that the inflorescence is terminal is fairly obvious in only a very small number of cases. It is especially clear in the Indian species *Caralluma pauciflora*, where each inflorescence lies right at the apex of the stem and consists of a single flower and three bracts (fig. 21 A). Such very reduced inflorescences are also typical of *Pectinaria* (fig. 21 B). In most inflorescences there are plenty of flowers and it is much harder to see that one of them is terminal (Wertel 1976). Only some measure of disturbance in the angles along the stem hints at what has taken place. The organization of flowers within these inflorescences was investigated by Wertel (1976), Bruyns (1988; 1993) and Meve (1994; 1997) but has been found stapeliads it is quite rare for any peduncle to develop. Peduncles of some length are found in several species of *Stapeliopsis*, occasionally

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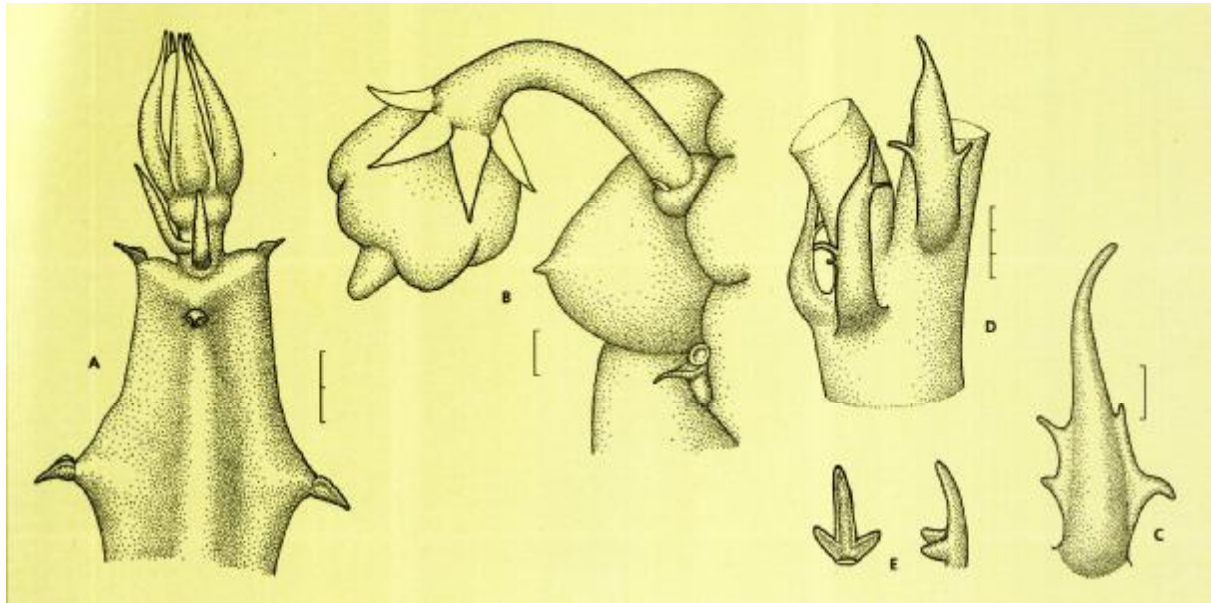


Fig. 21. Some very reduced stapeliad inflorescences (A,B.) and oddly shaped bracts found in some inflorescences (C-E). **A.** *Caralluma pauciflora* (PVB 5884). Each stem has a single inflorescence at its apex, which consists of a single flower (here a bud) and three slender bracts (one hidden here). **B.** *Pectinaria articulata* subsp. *asperiflora* (hort.). Each stem bears several tiny inflorescences each of which consists of a small bract with a swollen base and a single flower. **C.** bract from *Piaranthus atrosanguineus* (PVB 6538). **D.** part of inflorescence with several bracts from *Orbea melanantha* (PVB 6536). **E.** bract from inflorescence of *Hoodia officinalis* subsp. *officinalis* (PVB 3069) from front and side. Scale bars: A, 2 mm; B, 1 mm; C, 0.5 mm; D, 3 mm; E, 0.5 mm (at A).

in *Stapelia* and quite commonly in *Tromotriche*. The inflorescence mostly forms a patch against the stem from which the pedicels arise directly. Among the pedicels there are many small bracts. These sometimes have a swollen base and may even resemble the tubercles closely, as in *Larryleachia* and *Pectinaria*, but often they have one or more peculiar lateral teeth (fig. 21 C-E).

In the more leafy asclepiads, inflorescences are distributed along the upper parts of certain stems, which often elongate greatly during the flowering period. This also happens in many species of *Caralluma*. Amongst the stapeliads there are two basic positions in which inflorescences many land up.

(1) Near the apex of the stem. Plants producing apical inflorescences tend to have large numbers of them and the flowers are mostly small. These inflorescences may arise on the primary stem or on secondary stems. They are particularly prevalent in the northern genera, especially in *Caralluma*, but also occur in the southern hemisphere in most species of *Quaqua* (fig. 22 D), in *Baynesia*, *Hoodia* and *Larryleachia*.

(2) Near the base of the stem. These tend to be few per stem (usually only one) and the flowers may be very large and few in each inflorescence. Such inflorescences are found only on secondary stems (except in *Whitesloanea*). They are especially common

in species in southern Africa and also in the three genera (*Duvalia*, *Huernia* and *Orbea*) that are found in both north-east Africa and southern Africa (fig. 22 B).

In many species in a wide range of genera such as *Asclepias*, *Comphocarpus*, *Brachystelma*, *Sisyranthus* and *Hoya* the inflorescences consist of clusters of flowers which open almost simultaneously. In stapeliads this phenomenon is also found and has arisen several times independently in *Caralluma*, *Hoodia*, *Larryleachia*, *Orbea*, *Pseudolithos* and *Quaqua* (fig. 22 A, D). In some cases (e.g. *Caralluma speciosa*, *Quaqua mammillaris*) the flowers in these dense clusters are relatively large for the genus (i.e. this phenomenon is not restricted to the smaller-flowered species) and they are almost always very evil-smelling. All asclepiad inflorescences have bracts in them and even in relatively few-flowered inflorescences the axils of these bracts can become active and bear further flowers (Wertel 1976). Wertel's investigation showed that these dense inflorescences differed mainly in that whole 'sub-inflorescences' rather than single flowers arose in the axils of some bracts and that their development was relatively quick so that all the flowers are open nearly at once.

The flower

A casual examination of an asclepiad flower indicates that all the parts appear to occur in

multiples of five. In fact the female parts are paired, as are the laves, but this is not visible without dissection. It will probably be noted as well that the visible parts of the flower are all symmetric around several of the diameters (i.e. they are what is technically known as radially symmetric or actinomorphic), unlike the asymmetric flowers of, say, most orchids, which are symmetric only around a single axis (known as zygomorphic). This radial symmetry gives a false impression of simplicity. In fact the asclepiads have a remarkable and complex mechanical mode of pollination. For this their flowers exhibit a degree of specialisation for insect pollination which rivals that of the highly sophisticated flowers of the Orchidaceae.

Not only is the asclepiad flower extremely complicated, it is also very confusing; while sepals and petals can easily be found, little else that is familiar seems to be present. In particular, the stamens, anthers and pollen and the style, pistil and stigma all appear to be absent. The construction of the flower is not uniform among all asclepiads but the organisation of most of them can be extrapolated from an explanation of what is going on in a stapeliad flower. This will be illustrated and explained here by means of the example of *Orbea variegata* (fig. 23).

The sepals are readily located as small five, greenish, usually lanceolate lobes behind the flower. There are sometimes other tiny, partly transparent bodies usually grouped in clusters



Fig. 22. Different locations and numbers of inflorescences in the stapeliads. Inflorescence single towards base of stem: **A**, inflorescence with many $\pm$ simultaneously opening flowers, *Orbea albocastanea* (PVB 3543); **B**, inflorescence with 2 flowers, *Stapelia gettiffiei* (near Beauty, PVB). Inflorescences many towards apex of stem: **C**, *Stapelia paniculata* subsp. *paniculata* (PVB 6380); **D**, *Quaqua incarnata* subsp. *incarnata* (Yserfontein, PVB).



between the sepals and the base of the corolla. These are known as collectors (Kunze 1990).

In the stapeliads the corolla is always fleshy and somewhat rigid. The petals or corolla lobes are obvious and are generally relatively broad and short. This is in contrast to their often long, narrow and frequently complex shape in *Ceropegia*, although there are some exceptions to this among the species of *Caralluma* in north-eastern Africa. In the bud the lobes are valvate (i.e. the margins touch and do not overlap), unlike the position in many other asclepiads. At a very early stage the corolla possesses free

lobes and a short, congenitally fused part at the base. Only slightly later does marginal fusion of the lobes take place in the bud. Because this fusion takes place later than the formation of the lobes themselves; it is referred to as post genital (Endress 1994). In the mature stapeliad flower there is always a tube in the centre, though it may be very short. At its mouth or sometimes within the tube there is a ring of thickened tissue. This may be very prominent but it is sometimes just present as five swollen bumps beneath the bases of the lobes (fig. 24 A). It is assumed, at present without proof, that the

tubular part below the thickening (which will be termed the 'primary' tube) develops from the congenitally fused basal part of the bud. Any fused part (tubular or flat) outside the thickening forms a 'secondary' tube and is generated by post genital fusion of the lobes. In many flowers the lobes are divided right to the edge of this thickened area (fig. 24 A, H). In many others (as in species of *Hoodia* and in some species of *Huernia*) there is a further, united, flat to tubular area beyond the thickened region before the division into the lobes begins. So, for example, in *Hoodia parviflora* the funnel-

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shaped corolla tube consists of two parts: the primary, rather more steeply-sided tube around the gynostegium with a distinctly thickened mouth, and the secondary, more shallowly sloping tube beyond this thickened area (fig. 24 G). In *Hoodia gordonii* the secondary tube is usually flat outside the thickened mouth of the primary tube. A more extreme case is that of *Stapelia leendertziae*, where the secondary tube is almost globose and the primary tube is very short. In some species of *Huernia* there is a thickening around the middle of the tube and also a change in texture on the interior around the same point so that here, too, a primary and a secondary tube are present. However, this is not the situation in *Stapeliopsis neronis* (fig. 24 H), where the thickening in the corolla is

present immediately below the lobes and there appears to be no secondary tube. Some idea of the range of locations in these structures is provided in fig. 24.

These structures are not unique to the stapeliads. In most species of *Ceropegia* (exceptions exist, such as *C. dimorpha* and *C. meleagris*) the corolla tube consists of two parts: a basal inflation whose mouth is somewhat constricted (and often thickened), and above this a slender tube which continues until the lobes are reached. From the presence of an annular thickening in some cases around the mouth of the basal inflation, it seems reasonable to assume that the basal inflation is homologous to the primary corolla tube in the stapeliads and that the upper part of the tube corresponds to

the secondary tube in, say, *Hoodia parviflora* or the flat area in, for example, *H. gordonii*.

The annular thickening at the mouth of the primary tube is present to a very variable extent among the stapeliads and only rarely is it absent. In species such as *Piarranthus atrosanguineus* (and *Ophionella arcuata* in fig. 24), it is thickest below the sinuses of the lobes and fades away towards the middle of the lobe. Consequently the tube is distinctly pentagonal. In its early stages, the coralline corona lobes of, for example, *Leptadenia* also form a swollen bridge across the base of the lobes (Kunze 1990). Since other forms of coralline corona are entirely lacking in the stapeliads, it is possible that these annular thickenings are homologous to the coralline corona of *Leptadenia*. This ring-

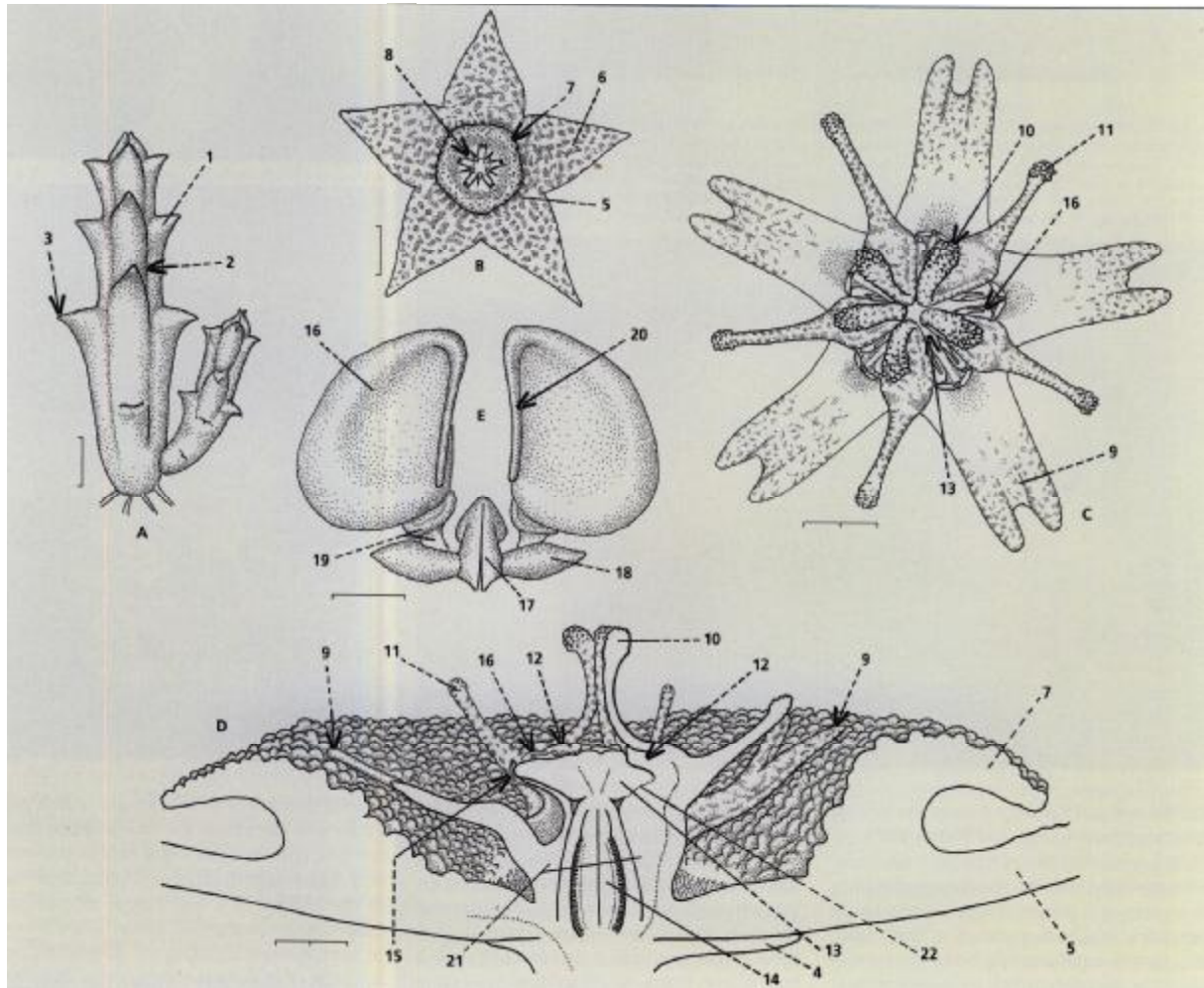


Fig. 22. Parts of a stapeliad (after White & Sloane 1937), based on *Orbea variegata*, with the pollinarium from *O. tapscotti*. A. stems; B. face view of flowers; C. gynostegium; D. half-flower, showing centre of flower only; E. pollinarium; 1= tubercle (podarium) on stem; 2= groove between vertical rows of tubercles; 3= leaf-rudiment; 4= sepal; 5= fused part of corolla below lobes forming secondary corolla tube; 6= corolla lobe; 7= annulus; 8= gynostegium; 9= outer corona lobe; 10= inner corona lobe; 11= dorsal horn of inner corona lobe; 12= anther; 13= style head; 14= ovary; 15= guide-rail; 16= pollinium; 17= corpuscle; 18= wing of corpuscle; 19= caudicle; 20= insertion-crest; 21= staminal tube; 22= retinacle. The dotted lines in D indicate vascular traces. Scale bars: A. 10 mm; B. 10 mm; C. 2 mm; D. 2 mm.

like corona 'annulus' has developed within the stapeliads to an extent not found anywhere else in the Apocynaceae. It varies from five discrete mounds (as in several *Hoodia* and *Piранthus* species) to a distinct, continuous, raised ring around the mouth of the tube. This ring may form a lip that projects inwards and begins to close up the mouth of the tube (*Tromotriche revoluta* and *Orbea conjuncta* fig. 24 D, F). The most extreme forms are found in *Orbea namaquensis*, *O. variegata* and especially in *O. ciliata* (fig. 10.91). In *O. namaquensis* and

centre of the flower, while in *O. ciliata* it is up to 11 mm long and forms a tube which easily equals the length of the actual corolla tube.

What appears to be a similar 'annulus' is present and conspicuous in several species of *Huernia* (*H. humilis*, *H. zebriana* etc.) and is often highlighted in addition by dramatic colours. Here the structure of the flower is slightly different (fig. 24 B). In these instances the prominence of the annulus is only slightly caused by a thickening of the fabric of the

below the lobes. This is therefore partly a false annulus and it is not entirely the same structure as in, say, *O. variegata*.

Stapeliad flowers vary from among the largest in the plant kingdom (up to 400 mm in diameter in *Stapelia gigantea*, Leach 1985) to very small indeed (2.5 mm diameter in *Pseudolithos caput-viperæ*, Bruyns 1990c). Almost all the flowers under 15 mm diameter are found in *Caralluma* and in the other genera

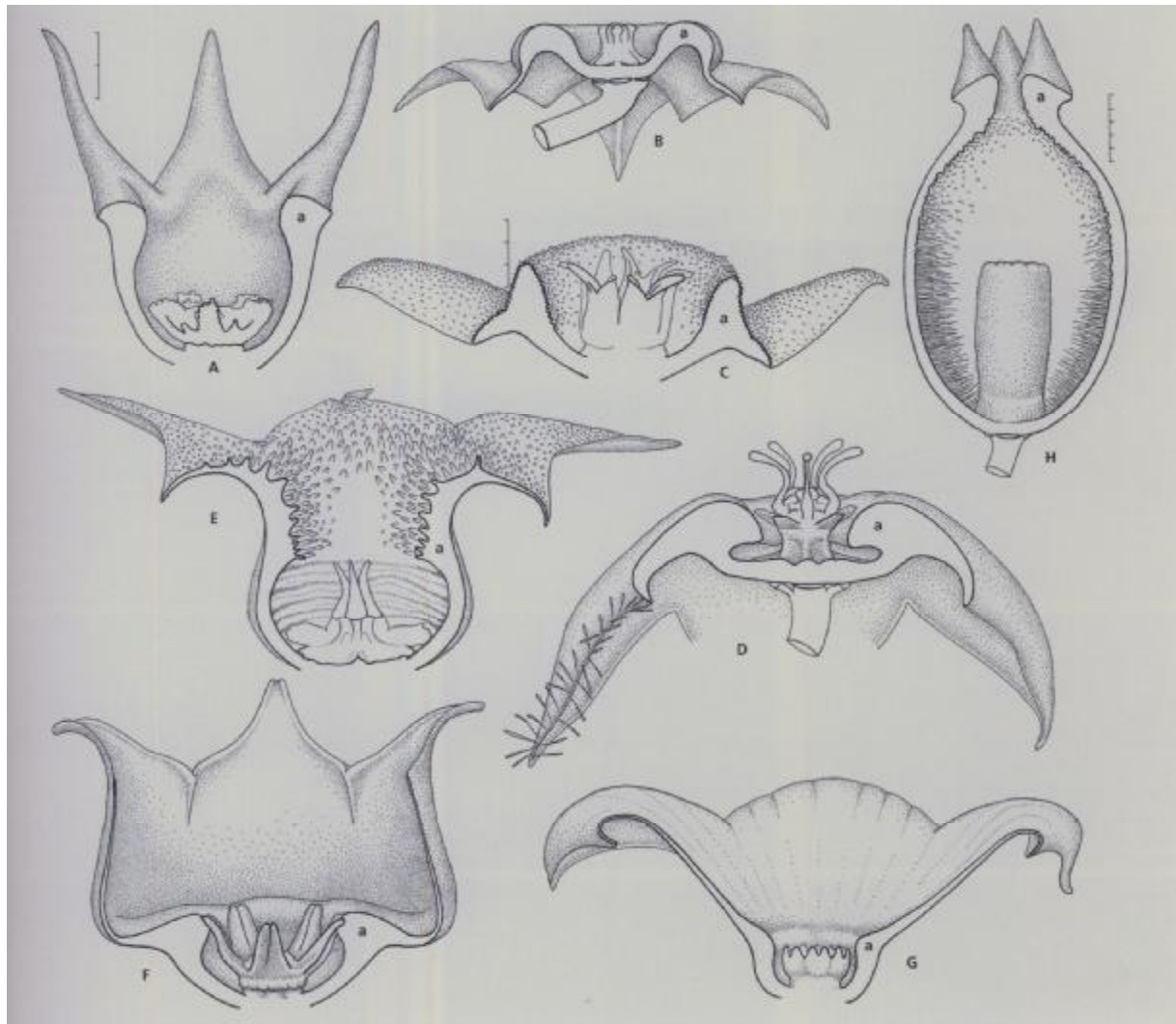


Fig. 24. Position of annulus (a = annulus), 'primary' tube (below annulus) and 'secondary' tube (between annulus and bases of corolla lobes) in various stapeliads.

A. *Ophionella arcuata* subsp. *mirkinii* (PVB 4257), annulus at base of lobes, tube made up entirely of primary tube, secondary tube absent. **B.** *Huernia humilis* (Heunis), annulus enclosing small primary tube, corolla reflexed beyond it so secondary tube absent. **C.** *Hoodia pilifera* subsp. *annulata* (KG 142/72), steep annulus enclosing very fine primary tube, secondary tube absent. **D.** *Tromotriche revoluta* (PVB 6021), large annulus enclosing small, flat-bottomed primary tube, corolla reflexed beyond it so secondary tube absent. **E.** *Huernia hislopii* subsp. *hislopii* (near Zaka, PVB), annulus present only as slight thickening in wall of tube, primary tube below it and secondary above, together forming quite large tube. **F.** *Orbea conjuncta* (PVB 6570), large annulus enclosing small primary tube, large secondary tube (with traces of fusion of lobes). **G.** *Hoodia parviflora* (PVB 4084), small annulus with small primary tube below it, very broadly spreading secondary tube above it forming most of diameter of corolla. **H.** *Stapeliopsis neronis* (PVB 2818), a very extreme case as in A. annulus at base of lobes, tube entirely composed of primary tube and secondary tube absent. Scale bars: A. 2 mm; B, D-H. 5 mm (at H); C. 3 mm.

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with many inflorescences toward the apex of the stem. Larger flowers are found especially in those genera with solitary inflorescences towards the base of the stem and are most common in *Stapelia*, where several species often produce flowers over 150 mm in diameter. The one exception among the 'apically-flowering' genera is *Hoodia* where the flowers may reach 180 mm in diameter. In most genera with large-flowered species there is a wide range of size and in *Stapelia* [his range is between 6 mm

(in *S. parvula*) and 400 mm (in *S. gigantea*). It is interesting to note, though, that such large flowers are actually very unusual among the asclepiads. Elsewhere they are known only in a few extremely rare, forest-dwelling species of the recently described genus *Calyptanthus* from Madagascar, where flowers of up to 100 mm in diameter have been recorded.

In many genera, there is particularly wide variation in the shape of the corolla. Corollas range from more or less flat to cupular with

in lobes about the same length as the tube and then, in more extreme cases, to variously cylindrical, spherical, ellipsoidal or urceolate. In some of these the lobes are reduced to tiny structures around the mouth of the tube and there is considerable variation in the extent to which the mouth of the corolla tube is constricted. The development of such cylindrical or urceolate flowers has taken place many times independently (Bruyns 2000a). They are encountered in *Ceropegia* and *Brachystelma* (e.g. *B. oianthum*) and within the stapeliads in *Echidnopsis*, *Huernia*, *Pseudolithos*, *Stapelia*, *Stapelianthus*, *Stapeliopsis* and *Tavaresia*.

The outside of the flower is mostly somewhat plainly coloured. It is not generally ornamented except for the existence in several genera (*Huernia*, *Ophionella* and *Pectinaria*) of obtuse papillae, each of which turn out, on close examination, to be an elevated stoma (fig. 25 C, D). The function of these is unknown. Papillae similar to those on the stems are found on the outside of all flowers in *Stapelia*. The relatively dull exterior is in complete contrast to the inside of the flower. Apart from the wide variety of shapes in stapeliad flowers, one of the main reasons for their fascination is the extraordinary variety of colours that one finds and richness of these colours. The complex textures of the surfaces also add to this richness, sometimes suggesting the intricate beauty of a fine Persian carpet.

On the inside the epidermal cells are arranged into a dense mosaic of variously bottle-shaped to conical or rounded cells (fig. 26). Among these so-called 'basal epidermal cells' there are other more elevated structures that repeat themselves in several unrelated genera. These were first surveyed by Ehler (1975).

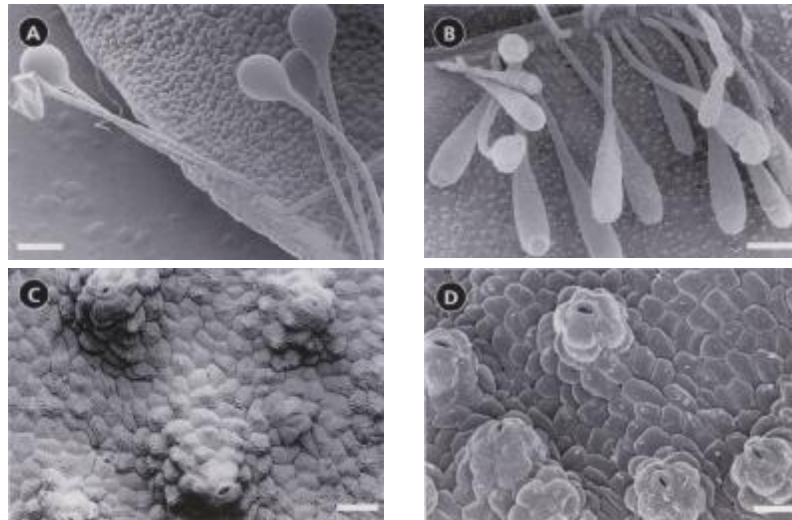


Fig. 25. Marginal cilia along corolla tubes near base and just along edge of carped of basal epidermal cells inside, with SAM. A. *Orbea rogersii* (PVB 6504); B. *Piaranthus decipiens* (PVB 6437), in young bud. Raised stomata on outside of corolla. C. *Huernia oculata* (PVB 5528); D. *Pectinaria articulata* subsp. *namaquensis* (PVB 6112). Scale bars (approx.): A. 250 µm; B. 500 µm; C-D 50 µm.

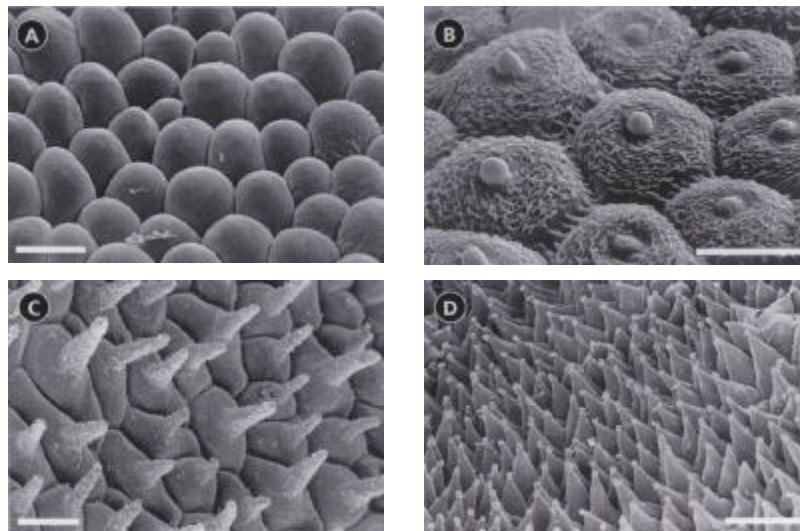


Fig. 26. Inner surface of corolla with SAM: basal epidermal cells. A. *Tromotriche pedunculata* subsp. *pedunculata* (PVB 5203). B. *Stapelia paniculata* subsp. *paniculata* (PVB 6173) C. *Stapeliopsis neronis* (PVB 5207). D. *Ophionella willowmorensis* (PVB 4966). Scale bars (approx.): A. B. 20 µm, C. 50 µm, D. 100 µm.

(1) Conical to cylindrical, multicellular papillae raised out of the surface.

These are covered with the usual epidermal cells except for the apical cell which is extended into a very variably shaped structure and usually has a distinctly roughened surface. These papillae are mostly 1-3 times as tall as thick but they reach an especially extreme form in *Stapelianthus* (fig. 27 F), where they are long and slender and superficially look just like the unicellular hairs found on flowers of, say, *Stapelia*. The apical cell on these papillae exhibits an astonishing variety of shapes. A selection of these papillae across various genera is shown in fig. 27 B-F, while the diversity in *Huernia* (where they are particularly common) is shown in fig. 28 A-E. They are considerably rarer in *Orbea* (fig. 29 B, D-F).

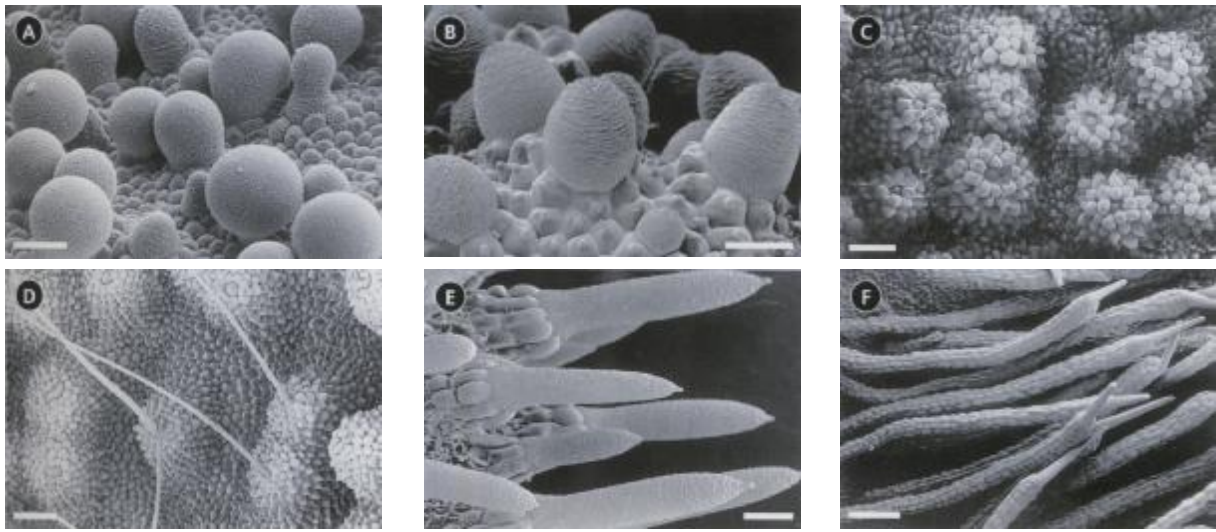


Fig. 27. Inner surface of corolla with SAM: structures among basal epidermal cells in several genera. **A.** *Tromotriche pedunculata* subsp. *pedunculata* (PVB 5203), papillae near centre of corolla. **B.** *Piaranthus punctatus* var. *punctatus* (Tulfontein, Ceres Karoo, PVB 7577) papillae on lobe and corolla. **C.** *Pectinaria articulata* subsp. *articulata* (PVB 5974). **D.** *Stapeliopsis urniflora* (PVB 5733), papillae near middle of tube, some with apical hairs and other with elongated, embedded apical cell. **E.** *Australluma peschii* (PVB 5498), papillae on lobes. **F.** *Stapelianthus montagnacii* (PVB 6203), papillae on lobe with very long shaft and small, apical 'hair'. Scale bars (approx.): A, B, 50 μ m, C-E 100 μ m, F, 250 μ m.

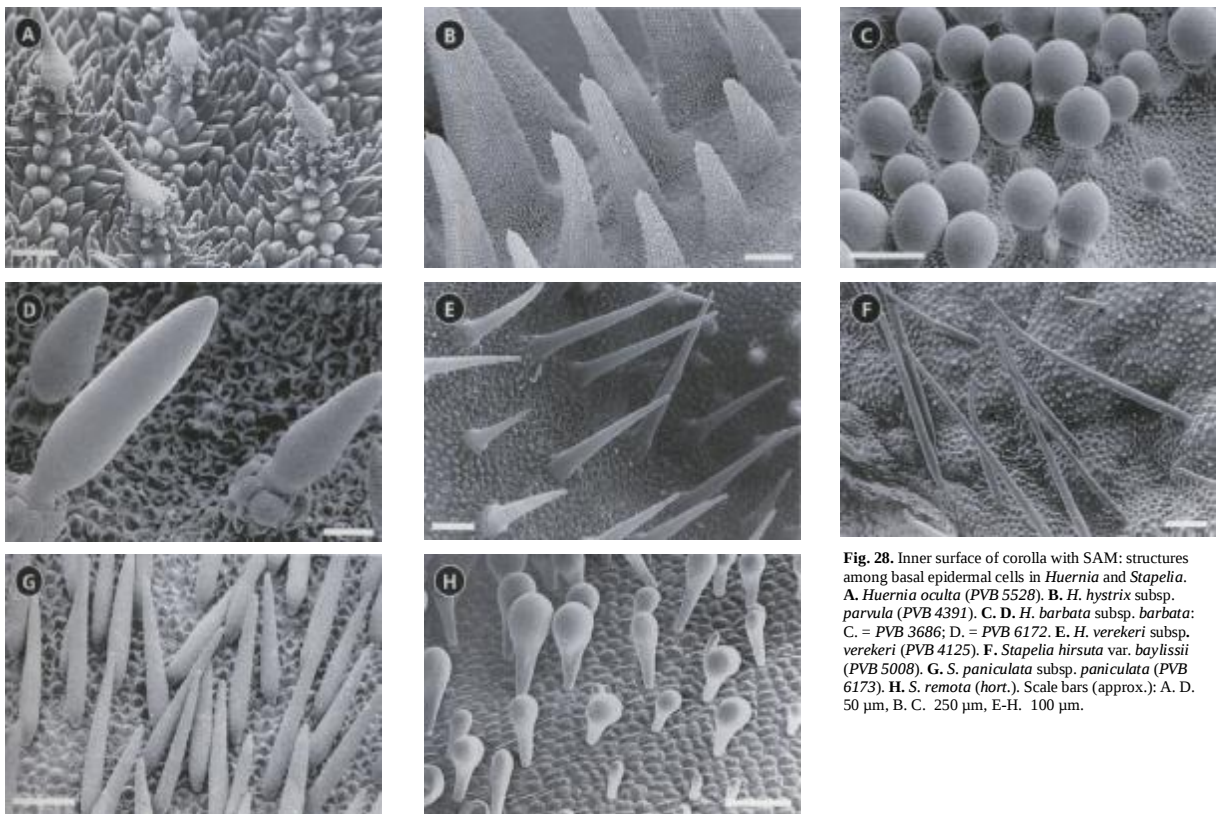


Fig. 28. Inner surface of corolla with SAM: structures among basal epidermal cells in *Huernia* and *Stapelia*. **A.** *Huernia oculata* (PVB 5528). **B.** *H. hystrix* subsp. *parvula* (PVB 4391). **C. D.** *H. barbata* subsp. *barbata*: **C.** = PVB 3686; **D.** = PVB 6172. **E.** *H. verekeri* subsp. *verekeri* (PVB 4125). **F.** *Stapelia hirsuta* var. *baylissii* (PVB 5008). **G.** *S. paniculata* subsp. *paniculata* (PVB 6173). **H.** *S. remota* (hort.). Scale bars (approx.): A, D, 50 μ m, B, C, 250 μ m, E-H, 100 μ m.

(2) The surface of the corolla is raised into ridges.

These are usually transversely arranged along the lobes and towards their bases and often vanish on the annulus, if this is present. In some cases, these ridges seem to be made up of many papillae of the type in (1) fused together, since what appear to be the larger apical cells often project randomly from them (see, for example *Tridentea vire-scens*). Such ridges are found particularly in *Orbea*, *Stapelia* and *Tromotriche* (fig. 29 A-B).

(3) Unicellular papillae raised out of the surface.

These are particularly common and hair-like in *Stapelia* (fig. 28 F-H). It is possible that these are the remnants of papillae such as in (1), where only the modified apical cell is now visible. Some very curiously shaped unicellular strictures are present in *Tromotriche* (fig. 27 A) and *Orbea hardyi*. It is appropriate to mention also the dense fringe of fine, hair-like papillae found right at the base of the tube in some species of *Orbea* (fig. 29 G-H). In the left-hand

corner of fig. 29 G a gradual change can be seen from tiny projecting cells to these hairs. Such hairs were first noted by N.E. Brown (1878) in *Orbea ciliata*. It is possible that these are homologous to the dense clusters of small hairs present in the tiny primary tube of some species of *Stapelia* (e.g. *S. clavicorona*)

(4) Vibratile cilia along the margins of the lobes (fig. 25 A-B).

These develop just along the edge of the dense carpet of epidermal cells that cover the inside of the corolla and just inside the line along which the lobes split at anthesis. Each cilium usually consists of several cells and is spindle-shaped, clavate or cylindrical. It has a very slender base and the apical cells are often enormously inflated. These cells are full of liquid before anthesis but usually this evaporates soon after the flower opens and then the cilium becomes flat, with the more clavate ones becoming spatulate on drying out. Once they are empty, they move in the slightest breeze and they are assisted in this by their extremely slender attachment to the corolla (Vogel 1961), which can be seen in fig. 25 A-B.

Right in the centre of the corolla is a complex crown-like object, which is often loosely referred to as the corona, but technically known as the gynostegium. A cursory examination of this suggests that it is made up of two series of lobes, each of which consists of five members. These lobes surround and partly cover a central column. The five lobes of the outer series (the outer corona lobes) are opposite the corolla lobes and are erect or spreading. The inner series (the inner corona lobes) alternates with the lobes of the outer series (and the corolla lobes) and here the lobes are mainly inclined

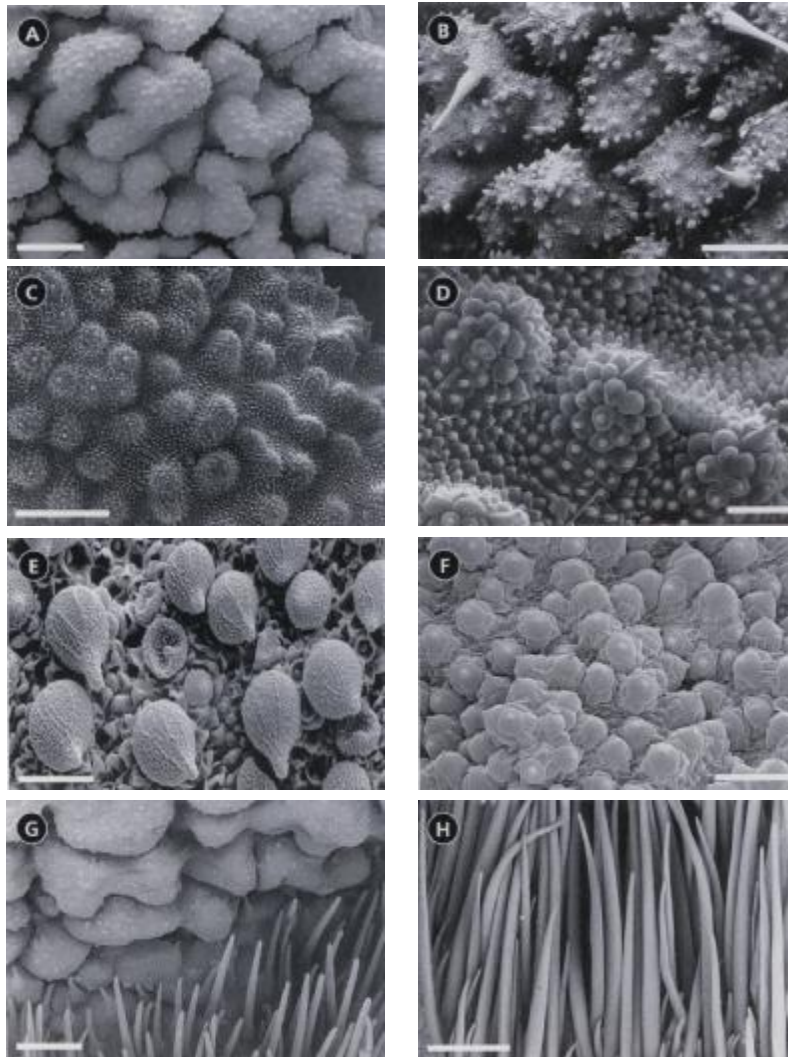
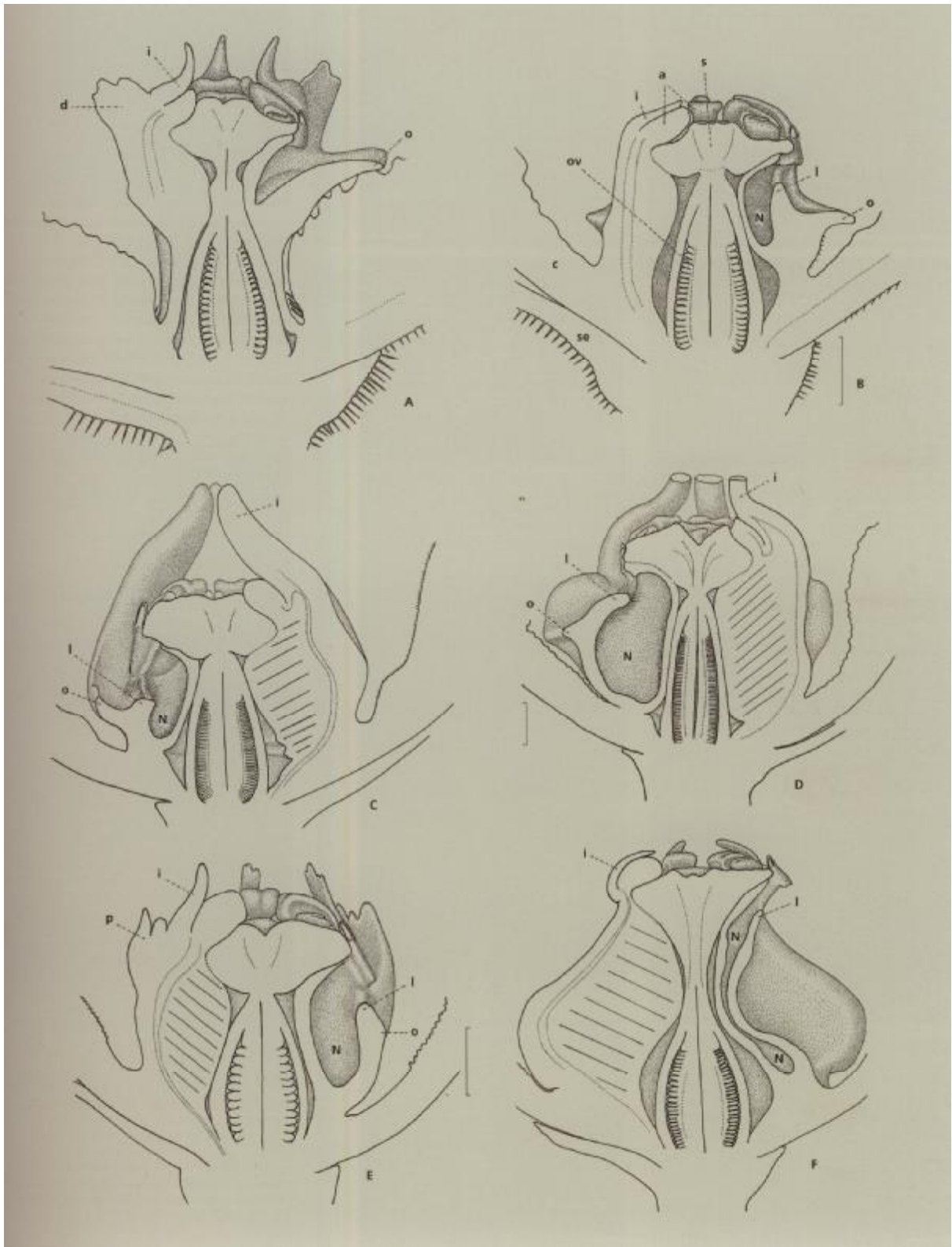


Fig. 29. Inner surface of corolla with SAM: structures among basal epidermal cells in *Orbea* and *Australluma*. **A**, deeply rugulose surface: *O. variegata* (hort.). **B**, deeply rugulose surface with some 'spikes': *O. carnosa* subsp. *keithii* (PVB 6590). **C-D**, papillate surface: *Australluma ubomboensis* (Hardy 5409). **E**, top-shaped cells: *O. carnosa* subsp. *carnosa* (PVB 6542). **F**, mammoses cells: *O. rogersii* (PVB 6504). **G, H**, bristles in base of corolla tube. In both case the base of the tube lies below the foot of the picture: **G**, *O. verrucosa* (PVB 5388); **H**, *O. ciliata* (PVB 6050). Scale bars (approx.): **A, B**, 500 µm; **C**, 400 µm; **D-E**, 50 µm; **F**, 100 µm; **G-H** 300 µm.

(Right) Fig. 30. Half-flowers showing outer corona and nectarial cavities enclosed by it. **se** = sepal, **c** = corolla, **o** = outer corona lobe, **I** = lip of outer corona growing up towards base of guide-rails to enclose cavity (absent in **A**), **p** = projection behind inner corona lobe derived from outer coronal series (present only in **E**), **i** = inner corona lobe, **d** = dorsal horn of inner corona lobe (present only in **A**), **N** = nectarial cavity (absent **A**), **a** = anther, **s** = style head, **ov** = ovary (some only shown in **B**, just for orientation and comparison with fig. 23). Dotted lines indicate vascular traces.

A, B, variation in *Stapelia*. **A**, *S. arenosa* (PVB 3748), outer corona consisting entirely of horizontal lobe with no enclosed nectarial cavity. **B**, *S. kwebensis* (PVB 3574) outer corona with short, horizontal lobe and vertical lip enclosing deep nectarial cavity. **C-F**, variation in *Piarranthus*. **C**, *P. decipiens* (PVB 6410), horizontal lobe longer than lip and nectarial cavity relatively small. **D**, *P. atrosanguineus* (PVB 6538), horizontal lobe short and lip much longer with large cavity behind it. **E**, *P. punctatus* subsp. *punctatus* (PVB 4042) horizontal lobe virtually absent and lip with large cavity behind it. **F**, *P. punctatus* var. *fransii* (PVB 4328), no horizontal lobe, cavity very long and pressed up against side of staminal tube. Scale bars: **A, B**, 1 mm (at **B**); **C, D**, 1 mm (at **D**); **E, F**, 1 mm (at **E**).



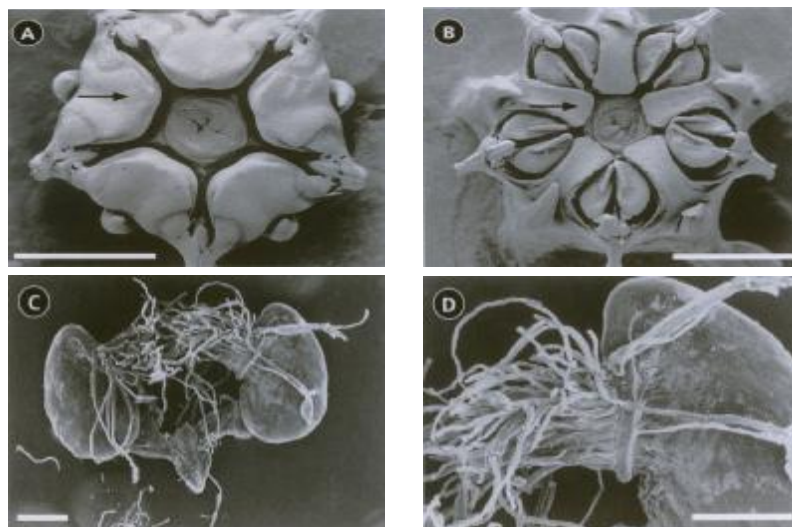


Fig. 31. A-B, late development of anthers (arrowed) in *Piaranthus punctatus* var. *framsii* (PVB 6070), with SEM. A, shortly before anthesis, anthers covering pollinia and partially obscuring base of corpuscle but beginning to tear away there. B, at anthesis, lateral margins of anthers shrunk back substantially to leave pollinia exposed. C-D, germinating pollinia with SEM, *Stapelia paniculata* subsp. *scitula* (PVB 6790) with D a close-up of right-hand

towards the centre of the flower.

The outer corona series may consist of five discrete lobes which usually spread away from the centre of the flower beneath the guide-rail. Alternatively by a process of fusion with the sides of adjacent inner lobes, each lobe forms a pouch between these adjacent inner lobes which at least to some extent surrounds the guide-rail. In other cases the outer series forms, by lateral expansion, a more or less continuous spreading ring around the gynostegium; this is especially noticeable in *Duvalia* and some *Huernia*, and even in *Orbea schweinfurthii*.

In a few places in the literature certain species of stapeliad have been said to have a 'uniseriate' corona and in these species invariably the outer series is said to be absent. Perhaps the best example is provided by *Piaranthus* (White & Sloane 1937; Meve 1994) but this is also the case in *Duvaliandra* (Gilbert 1980) from Socotra and in *Orbea maculata* (White & Sloane 1937: 337, 340-341). Among related genera this has also been stated to be the case in *Brachystelma burchellii* (Meve & Liede 2001 a). However, detailed studies of the early stages of these structures always reveal that the outer series of lobes is present but it remains small and in later stages becomes

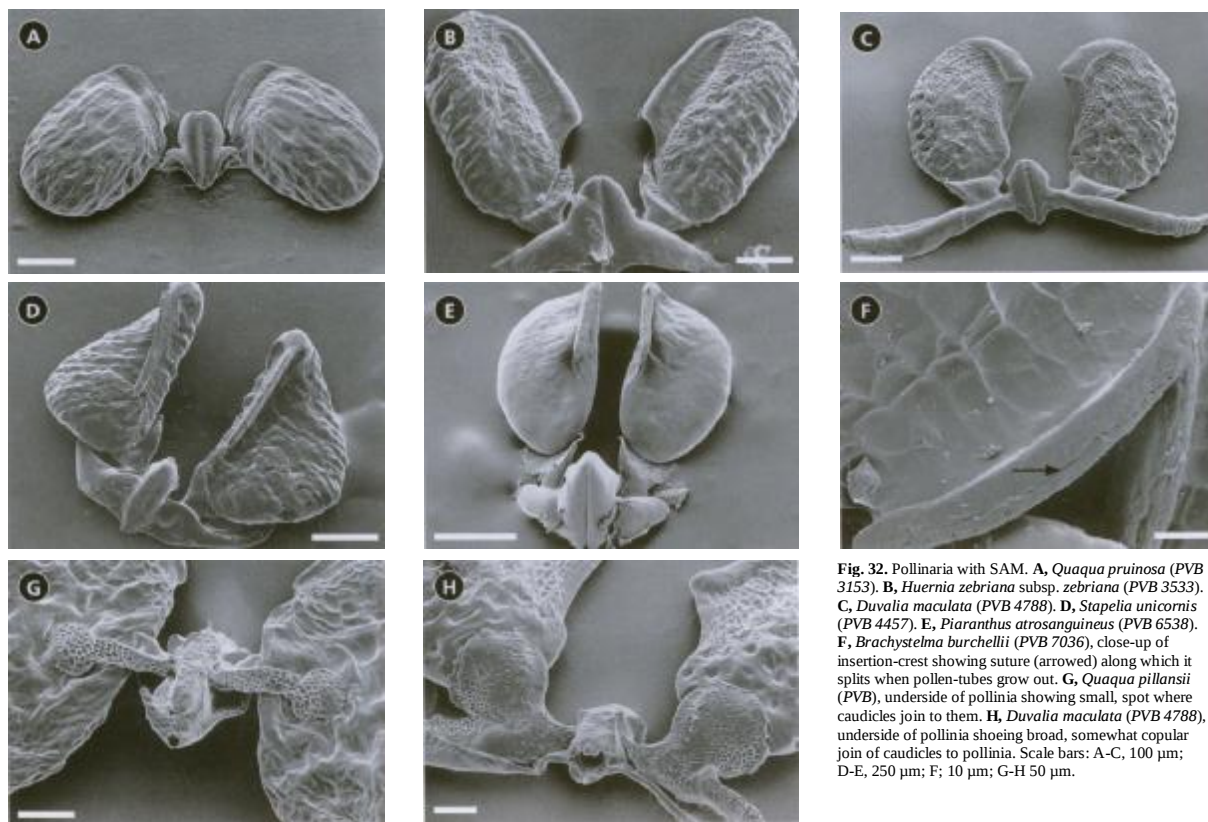


Fig. 32. Pollinaria with SAM. A, *Quaqua pruinosa* (PVB 3153). B, *Huernia zebriana* subsp. *zebriana* (PVB 3533). C, *Duvalia maculata* (PVB 4788). D, *Stapelia unicornis* (PVB 4457). E, *Piaranthus atrosanguineus* (PVB 6538). F, *Brachystelma burchellii* (PVB 7036), close-up of insertion-crest showing suture (arrowed) along which it splits when pollen-tubes grow out. G, *Quaqua pillansii* (PVB), underside of pollinia showing small, spot where caudicles join to them. H, *Duvalia maculata* (PVB 4788), underside of pollinia showing broad, somewhat copular join of caudicles to pollinia. Scale bars: A-C, 100 µm; D-E, 250 µm; F, 10 µm; G-H 50 µm.

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Fig. 33. Insertion of pollinia (arrowed) in guide-rails, showing different orientation depending on orientation of insertion-crest on pollinium with SEM. **A**, *Duvalia corderoyi* (PVB 6275). **B**, **C**, *Orbea verrucosa* (PVB 5388). Scale bars: **A**, **B**, 500 μ m; **C**, 250 μ m.

obscured by the much larger inner corona lobes. This was discussed extensively in the case of *Piaranthus* in Bruyns (1999b). Thus, in fact, there are no known stapeliads in which the outer corona is absent.

A peculiar phenomenon associated with the outer corona is the development in some

species of a cavity in the tissue towards its base, below the base of the guide-rail. This structure is unique to the stapeliads and referred to here as the 'nectarial cavity'. Various examples are shown in fig. 30, 34. Nectar tends to collect in the cavity after running down from inside the guide-rails but there is no evidence that the

cavity itself produces nectar, despite its often very papillate inner surface (see fig. 34 D, E). These cavities range from more or less absent (e.g. some *Stapelia*) to very deep indeed and may reach nearly to the base of the gynostegium. The mouth of the cavity is to some extent closed off by a flap of tissue of the outer corona. This

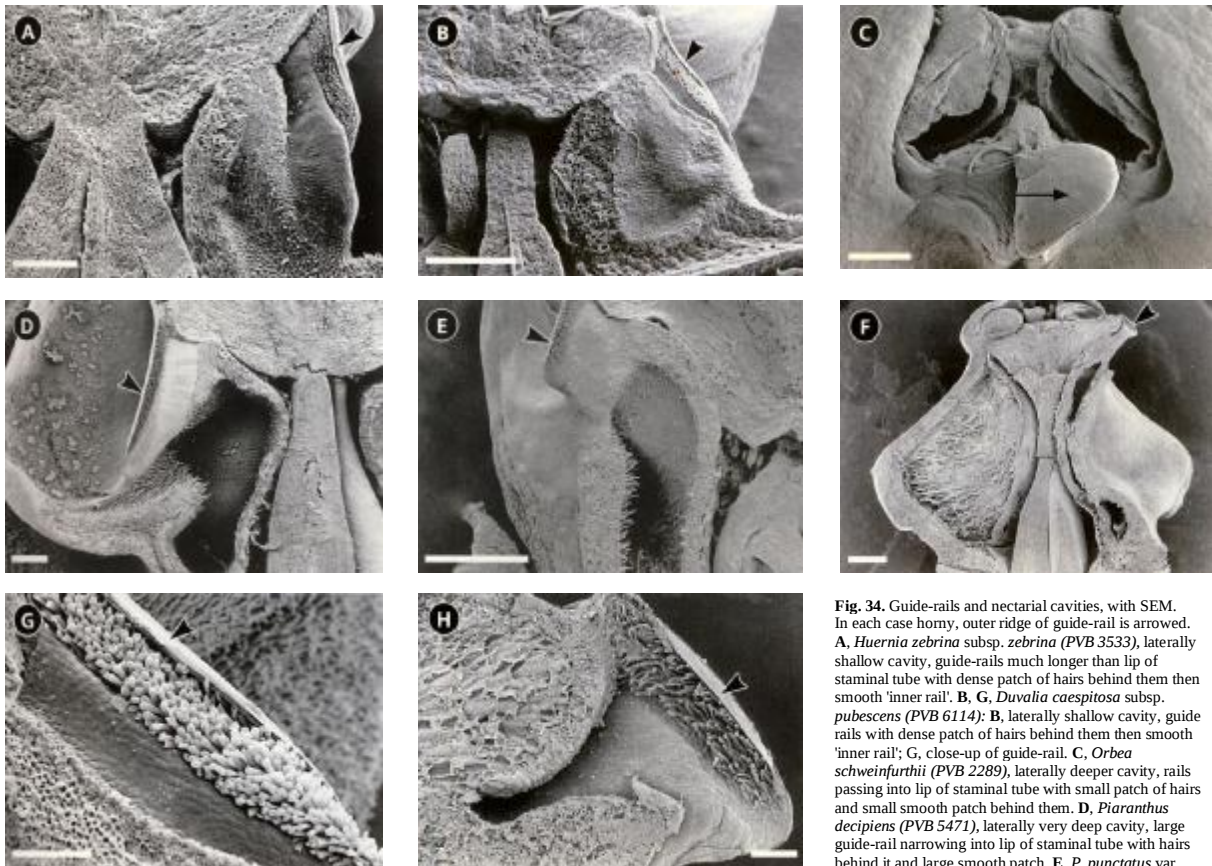


Fig. 34. Guide-rails and nectarial cavities, with SEM. In each case horny, outer ridge of guide-rail is arrowed. **A**, *Huernia zebrina* subsp. *zebrina* (PVB 3533), laterally shallow cavity, guide-rails much longer than lip of staminal tube with dense patch of hairs behind them then smooth 'inner rail'. **B**, **G**, *Duvalia caespitosa* subsp. *pubescens* (PVB 6114): **B**, laterally shallow cavity, guide rails with dense patch of hairs behind them then smooth 'inner rail'; **G**, close-up of guide-rail. **C**, *Orbea schweinfurthii* (PVB 2289), laterally deeper cavity, rails passing into lip of staminal tube with small patch of hairs and small smooth patch behind them. **D**, *Piaranthus decipiens* (PVB 5471), laterally very deep cavity, large guide-rail narrowing into lip of staminal tube with hairs behind it and large smooth patch. **E**, *P. punctatus* var. *framesii* (PVB 6070), very deep cavity, guide-rail much narrowed into lip of staminal tube, with hairs and smooth patch. **F**, **H**, *P. punctatus* var. *framesii* (PVB 4328): **E**, cavity flattened against staminal tube; **H**, guide-rails with hairs and smooth area merging into lip of staminal tube. Scale bars (approx.): **A**, 250 μ m; **B**-**E**, 500 μ m; **F**, 1 mm; **G**, **H**, 100 μ m.

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flap is slightly displaced outwards in most species of *Huernia* to produce a small tubercle below the guide-rail which quite effectively hides the entrance of the nectanial cavity. In *Piранthus* (and in some species of *Orbea*, such as *O. maculata*) there is a gradual loss of the lip of outer corona with the growth of the lip of the cavity. This reduction reaches an extreme form in *Piранthus* where several species lack the limb entirely, though they have a very deep nectanial cavity. The very peculiar case of *P. punctatus* var. *francesii* is illustrated in fig. 30 F and fig. 34 F.

The inner corona always consists of five discrete lobes and the only case where they are entirely missing is that of *Caralluma solenophora* from Arabia. In almost all cases they are adpressed to the backs of the anthers (the one notable exception being *Caralluma sinaica*) and they are mainly dorsiventrally flattened. Many of them rise up in the centre of the flower beyond the anthers where, together, they form a small column. In a few cases they are quite noticeably swollen and clavate (*Stapelia clavicornata*, *S. remota* and several species of *Tromotricha*) or flattened above (*Whitesioanea crassa*). In *Orbea*, *Stapelia*, *Tridentea* and *Tro-*

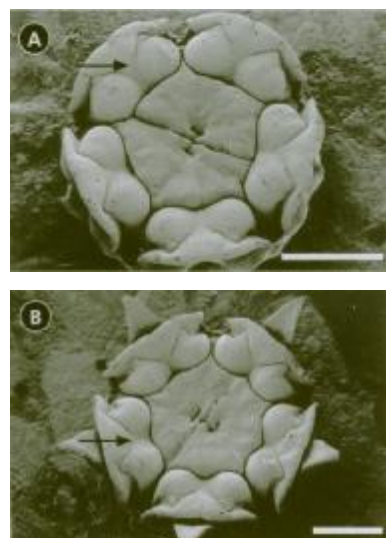


Fig. 35. Views of the gynostegium from above, showing development of anthers (arrowed), style head and corona in *Stapelia obducta* (PVB 4977). In both, the anthers are erect alongside the style head while later they grow over its summit and become horizontal on top of it. The corona lobes are at an early stage of their development. **A.** An earlier stage. The five anthers are clearly visible, each with two bulging sacs in which the pollinia are developing. The style head in the centre shows clear division into two parts with two small depressions corresponding to the top of the carpels beneath. The edge of the style head is pentagonal from pressure from the anthers. **B.** Here inner corona lobes are just beginning to be visible around backs of the anthers and the style head is less obviously divided into two parts. Scale bars: A, B, 1 mm.

motriche they often bear a flattened, fin-like dorsal horn. The whole lobe is laterally flattened in *Stapeliopsis*.

Under a magnification of 10-20 times it can be seen that, beneath each inner lobe, pressed into the top and sides of a central, whitish cushion (the style head) is a small yellowish body which is usually rectangular or square in outline with a lateral cavity ('theca') on either side. This body is the anther and each anther gives rise to two swollen pollen masses, or pollinia, one on either side. When the flower is fully open the pollinium appears to lie partly outside the lateral cavity in the anther which gave rise to it. In the early stages, the pollinia are in fact entirely hidden within the anther. Somewhat before anthesis the anther splits along its sides and its lateral margins shrink back to expose the pollinia. This is shown in fig. 31 A, B. More or less midway between adjacent anthers, on the edge of the style head, there is a small, shiny, dark brown object, which is termed the corpuscle. Directly beneath each corpuscle there is a vertical ridge of somewhat hard, rigid and slightly translucent tissue that runs downwards towards the base of the flower and narrows towards the base. Each ridge has a fine groove running vertically up its middle and the ridge with the associated groove is termed the guide-rail. The base of the guide-rail is usually slightly flared like a small mouth (fig. 31 B, fig. 33 A) and, if the microscope is good, it may be possible also to observe that the groove of the guide-rail is confluent with a fine vertical groove in the corpuscle. There are therefore five corpuscles and five guide-rails per flower.

If one attempts to remove a corpuscle with a fine pair of tweezers, two interesting things can be observed. Firstly it is a hard, amber-like body. It has been shown that it is not made up of cells but is secreted by part of the style head as a liquid which then hardens into this form (Demeter 1922; Schill & Jakel 1978; Kunze 1993). Such secretions of the style head are present more widely in the Apocynaceae (Endress & Bruyns 2000: 29) but it is only in the Asclepiadoideae and Secamonoideae that they harden into a corpuscle. Secondly, if it is pulled gently and the structures attached to it are not broken off, it will emerge with quite a lot of extra baggage. If examined under higher magnification (x30-80), what comes out with the corpuscle will be found to look more or less as in fig. 23 E and fig. 32 A-E. This whole object is called a pollinarium. The corpuscle has two more or less transparent wings on either side. To the underside of each of these wings a fairly pliable yoke is joined. This is also more or less transparent and is termed the caudicle. The caudicle passes from the wings on the corpuscle to the underside of the pollinium (fig. 32 G, H). Both the wings and the caudicles are also secreted by the style head, so that they, like the corpuscle, are products

of the female part of the flower. It cannot be seen by this method, but in fact the pollinium is a compartmentalized sac where each compartment is inhabited by a single, rather elongated pollen grain (Volk 1950). Scrutiny of the pollinium shows that, towards its outer edge, it has a translucent ridge along most of its length. This ridge is variously termed the insertion-crest, germination mouth or pellucid margin. When germination of the pollen takes place, this ridge splits longitudinally along the suture that is present there (fig. 32 F) and the pollen tubes all emerge from the slit that develops (fig. 31 C, D), as Volk (1949) found. This process is different in other groups of the Asclepiadoideae. In the Asclepiadeae and the Marsdenieae there is mostly no insertion-crest and the pollen tubes break out in various sites on the pollinium, depending on the genus. On the other hand, in the Gonolobinae, an entirely American group within the Asclepiadeae, there is usually an insertion-crest but the pollen tubes do not grow out through it, emerging rather through one somewhat concave side of the pollinium (Kunze 1995b).

If one were to observe carefully what happens while the pollinarium is removed, one would notice that each pollinium emerges from a slit on the side of a different anther and the pollinarium therefore brings together pollen from two adjacent anthers.

Within the stapeliads there is more or less no variation in the structure of the pollinarium i.e. in the presence or absence of its constituent parts. This is quite different to the position, for example, in *Hoya*, where there is fairly wide variation in the structure of the pollinarium (Rintz 1978). Variation occurs rather in the relative sizes of the constituent parts e.g. longer corpuscle relative to pollinium, the size of the pad joining the caudicle to the underside of the pollinium and especially in the shape of the pollinia. In the genera with small pollinia ($\pm < 0.30$ mm long or broad), they are generally ellipsoidal and broader than long to occasionally longer than broad. In the genera with larger pollinia they are mostly D-shaped (with the insertion-crest along the longest edge). Exceptions are *Ballyanthus*, *Duvalia*, *Duvaliandra*, *Huernia* and *Whitesioanea*, where they are ellipsoidal but longer than broad. A selection of pollinaria is shown in fig. 32.

Perhaps the most obvious variation is to be seen in the size of the pollinia. In *Ceropegia* and *Brachystelma*, pollinia are generally small and never reach more than half the length of the larger stapeliad pollinia. Some species of *Ceropegia* have fairly ornate corpuscle and wings but in most of them these organs are also small. Small pollinia are found in the northern hemisphere especially in *Caralluma* and *Echidnopsis* and in *Baynesia*, *Ophiocnema*, *Pectinaria* and *Quaqua* in the southern hemisphere. Larger pollinia are found in the

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southern genera, although the three genera common to both the north and the south have larger pollinia. The largest pollinia are found in *Tromotriche revoluta* (where they are known up to 0.95 mm long), *Tavaresia angolensis* (up to 100 mm) and *Orbea namaquensis* (up to 1.20 mm) and these are all D-shaped. These are not by any means the largest pollinia in the asclepiads and considerably larger pollinia are found in the Asclepiadeae. Even in the small-flowered genus *Microlooma*, the pollinia are up to 1.20 mm long and in *Pachycarpus* and *Parapodium* they reach 1.75 mm long.

Another feature that is almost exclusive

to the small-flowered genera of the stapeliads is the location of the insertion-crest exactly along the outer edge of the pollinium (fig. 32 A). When such a pollinium is inserted in the guide-rail, it stands straight out along a radius of the flower (fig. 33 A). In most of the larger-flowered genera the insertion-crest twists towards the outer surface of the pollinium (fig. 32 D, E). When such a pollinium is inserted in the guide-rail, it lies somewhat against the rail rather than projecting outwards along a radius of the flower (fig. 33 B, C). It is therefore possible for the outer corona to be formed much closer to the guide-rail than would otherwise

be possible. A reversion to the situation where the insertion-crest lies exactly along the edge of the pollinium occurs in *Ballyanthus*, *Duvalia*, *Duvaliandra*, *Huernia* and *Whitesloanea* (fig. 32 B, C). Here the inner and outer coronas are widely separated again and there is plenty of space around the guide-rail for the pollinium to spread outwards.

A typical angiospermous stamen consists of a filament and an anther. The anther is divided into two thecae, each of which consists of two locules that bear the pollen. When compared with this, the stamen in a typical stapeliad is a highly modified structure.



Fig. 36. Follicles (seed-horn) on various stapeliads.
Slender follicles: A, *Quaqua linearis* (PVB 6180); B, *Hoodia officinalis* subsp. *delaetiana* (PVB 7903).
Stouter follicles: C, *Larryleachia perlata* (PVB 8385) where the follicles are somewhat adpressed to the stems;
D, *Orbea variegata*, Table Mountain, Cape Town.



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A carefully dissected half-flower (as in fig. 23 D) is useful in understanding the relationship of the anther to the rest of the gynostegium and the coronas. Since there are only two ovaries, there is only one cut that will break the flower vertically into two equal halves. If one can make such in dissection, a lot more becomes clear.



Fig. 37. Two follicles with their covering removed to show the dense packing of the seed inside, *Tromotriche revoluta*, PVB 6036, Botterkloof.



Fig. 38. Beginning of release of seed from the follicles in *Stapelia obducta*, PVB 7038, Groot Winterhoek Mountains

The filament is not apparent in any of the half-flowers. Although it has often been stated that the tube around the ovaries is formed by lateral fusion of the filaments (Demeter 1922; Kunze 1990; 1996), there is actually no proof of this and it remains unclear exactly which tissue has given rise to this tube. There is even evidence to suggest that the filaments, which are present, if small, in many other Apocynaceae, many have been lost entirely in the Asclepiadoideae and the Secamonoideae (Endress & Bruyns 2000). Although it is possible that the corolla has contributed to the lower part of this tube, it is taken to be mainly staminal in origin and so it is referred to as the staminal tube. It is now generally agreed that the dorsal

locule (pollen sac) of each theca is reduced in the Asclepiadoideae and that only the ventral locules are fertile. Consequently in the Asclepiadoideae each anther produces only two pollinia (Demeter 1922; Kunze 1996). This is not true elsewhere in the Apocynaceae and even in the Secamonoideae each anther produces four pollinia. From the half-flowers (fig. 23 D, fig. 30) it can be seen that the staminal tube is fused to the style head just below the fertile part of the anther. This region of fusion is known as the retinacle and the strength of this fusion and the rigidity that it lends to the entire gynostegium is extremely important for its functioning in pollination. It is also reasonably obvious from these diagrams that the various corona lobes on

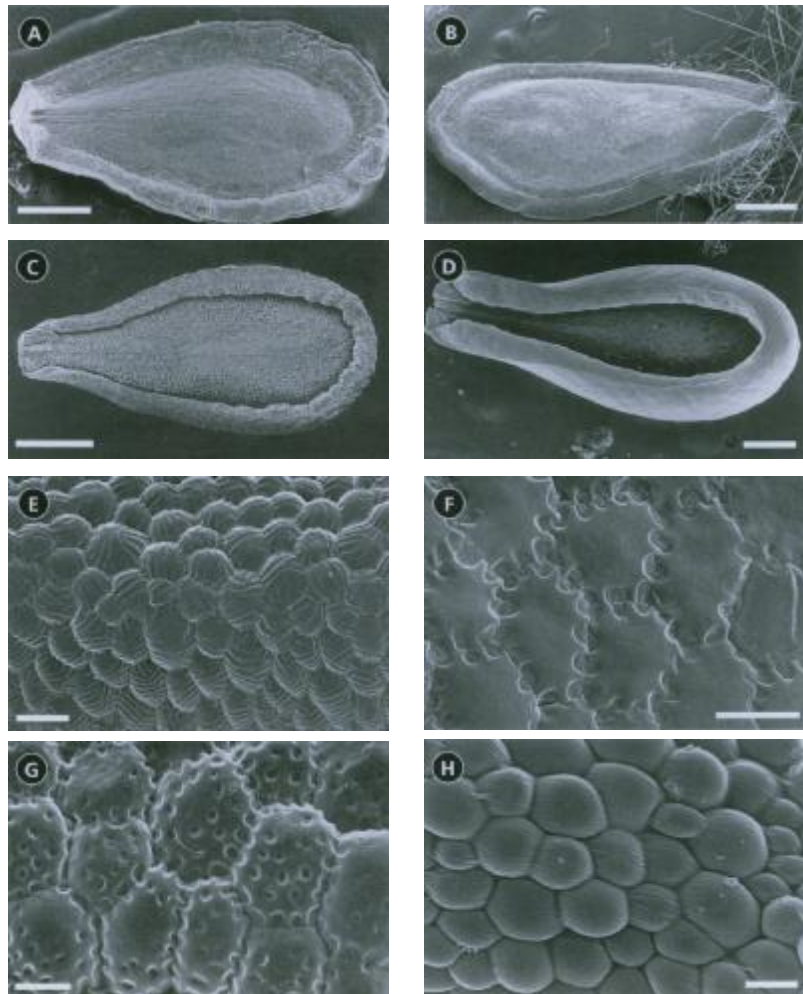


Fig. 39. Seeds of stapeliads, with SEM. Ventra view of whole seed. A, almost flat seed, *Tridentea virescens* (PVB 3448). B, almost flat seed with some sub-marginal hairs (which arise on dorsal surface), *Larryleachia marlothii* (Heunis 17). C, boat-shaped seed with margins folded inwards, *Tromotriche choanantha* (PVB 2907). D, boat-shaped seed with margins more strongly folded in ways, *Stapelia hirsuta* var. *hirsuta* (Mitchellis Pass, PVB). Sculpturing of surface of cells on margin. E, *Larryleachia picta* (Heunis 3). F, *Hoodia alstonii* (PVB 4646). G, *Larryleachia tirasmontana* (Heunis 6). H, *Quaqua arenicola* subsp. *pilifera*, with $\pm$ no sculpturing (PVB 4015). Scale bars: A-D, 1mm; E, F, H, 50 μ m; G, 50 μ m.



Fig. 40. Embryos of some Asclepiadoideae. Seed soaked for ± 24 hours then embryo removed. c = cotyledon; h = hypocotyl. **A**, *Brachystelma austral* (PVB 4420), large cotyledons with petiole, hypocotyl $\pm$ absent. **B**, *Hoya pauciflora* (PVB 5946), extremely small seeds so whole structure very small. **C**, *Cynanchum perrieri* (PVB 6227), large cotyledons but no petiole, small hypocotyl. **D**, *Ceropegia filiformis* (PVB). **E**, *Frerea indica* (PVB 5925), large cotyledons, hypocotyl enlarged. **F**, *Orbea halipedicola* (PVB 7401), cotyledons reduced, (PVB 8028), cotyledons $\pm$ absent, hypocotyl taking up almost whole embryo. Scale bars: **A-H**, 1 mm (at **A**).

the gynostegium are products of this staminal tube and that the inner corona lobes arise high up on this tube at the base of the anther while the outer lobes mostly arise nearer to the base of the tube.

Below the edge on the style head that secretes the corpuscle, one half of the guide-rail can be seen in the half-flowers. If this is examined carefully (it is generally hard to see much fine detail on it with a dissecting microscope) it will be found to consist of an outer, usually vertical, very much hardened ridge projecting out slightly towards the observer. Behind this ridge the tissue is slightly depressed and usually somewhat papillate, after which there is usually a smooth patch until the edge of the style head is reached (fig. 34). Parts of this depressed area are responsible for the secretion of small amounts of nectar. This nectar often runs down from the guide-rail and spreads out in the cavity below it or onto the corona. The guide-rails are produced by strong downward extensions and internal hardening of the lateral margins of the anthers (Kunze 1982). This elongation gives the anthers a peculiar swallow-tailed shape that is

unique to the asclepiads and some members of the Apocynoideae.

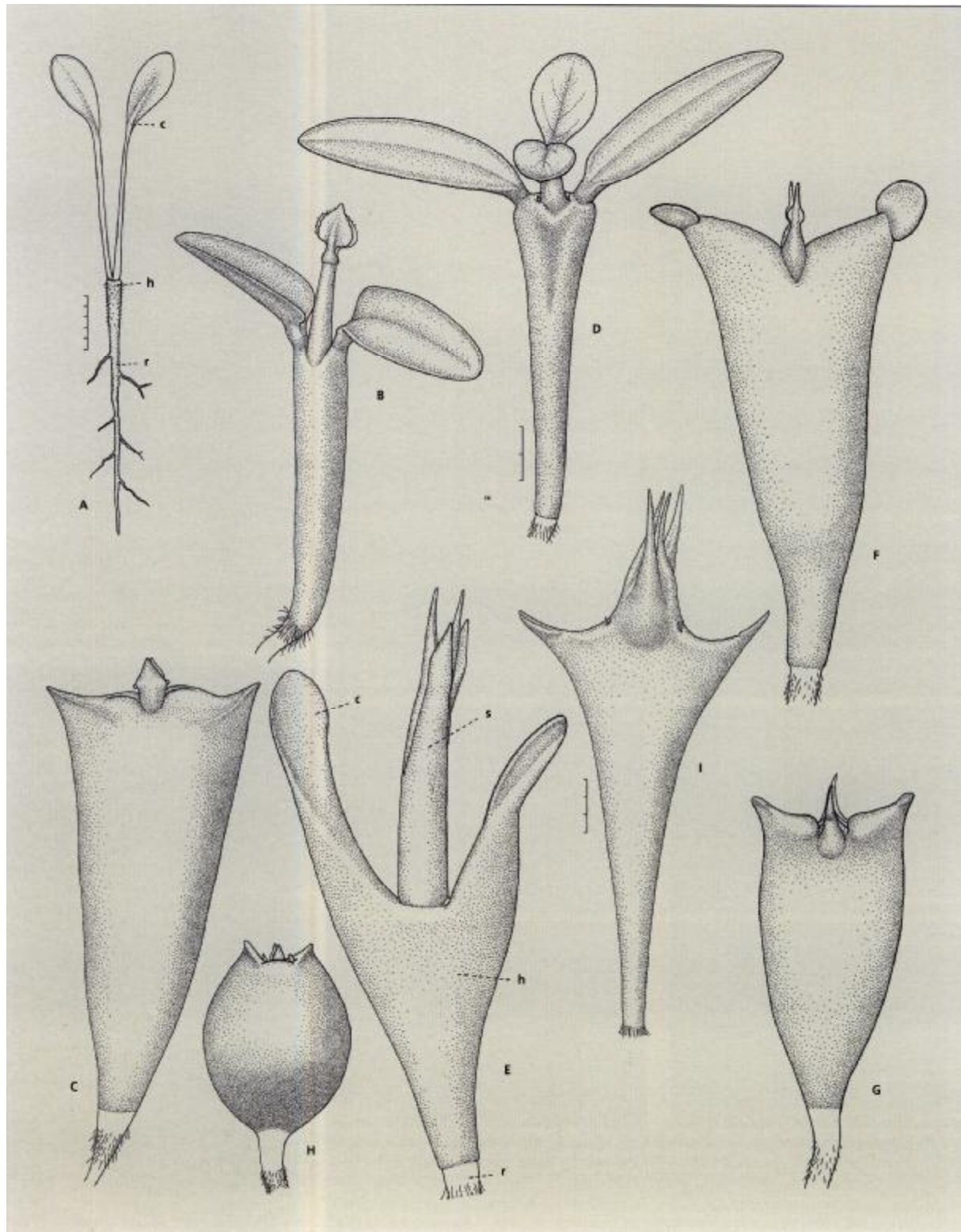
In the stapeliads then, the stamens form a tube around the ovaries which bears the corona lobes. The filament has been lost and the anther is reduced to two locules that produce altogether two pollinia. The anther also contributes the guide-rail.

From the half-flower the style head is now seen as a thick structure which blocks the mouth of the staminal tube and is joined to the two ovaries by a short, narrow neck. This and the two ovaries are all that remains of the female parts. The left-hand side of the style head (in fig. 23 D) is more elongated and it has been shown that the outer edge of this is responsible for the secretion of the corpuscle and its wings and for joining these up to the pollinia (Demeter 1922). On the right-hand side (fig. 23 D) the top of the style head is heavily indented by the anther, which is more or less horizontally inflexed on the style head. The manner in which the anthers are pressed into its sides (fig. 35) gives it a pentagonal outline which is misleading, since it is actually made

up of only two parts corresponding to the two ovaries (Demeter 1922). These two parts start off separate but they fuse during the development of the flower and later the regions of fusion are practically invisible (Endress 1994). Consequently, at anthesis the style head gives the impression of being a single body, though the separate vascular traces are usually visible on dissection. The central area of the style head beyond where the anthers are embedded (i.e. its apex) is generally a little raised. It very rarely almost equals the height of the anthers and is never extended beyond them as one finds in some of the Asclepiadeae (e.g. Bruyns & Linder 1991 for *Microloma*; Bruyns 1999f for *Eustegia*). The apex of the style head is generally flat to a little depressed with a cross-like indentation in the centre (sometimes just two deeper indentations) reflecting the two carpels below it. For information on which part of this structure is receptive, see 'Mechanics of Pollination'.

While the style head is of relatively uniform shaped throughout the stapeliads, one deviating trend is to be found in two entirely different places, namely in *Pseudolithos* and in the

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genera *Stapelianthus* and *Tavaresia*. In these the style head becomes concave above and is thin and somewhat plate-like, with the spots secreting the corpuscles raised considerably above the centre and often above the anthers as well. Here the anthers are pressed into the concave part of the style head and consequently they descend towards the centre of the flower (where they are ascending or more or less horizontal in all other stapeliads).

Several of the organs found in the asclepiad flower are refinements and specialisations of those that are present in the apocynaceous flower. Guide-rails are present, for example, in *Adenium* and *Pachypodium* and some small inner coronas are found in certain apocynacs such as *Vallaris heynei*. Even the 'translator' that led Robert Brown (1810) to split off the Asclepiadaceae from the Apocynaceae has been found in rudimentary form in some apocynacs (Endress & Bruyns 2000: 29). However, in degree of modification and specialisation that is not found elsewhere. Both the outer corona and the corpuscle are not found outside the Asclepiadoideae and the Secamonoideae. The construction of the corpuscle and guide-rail is similar throughout the stapeliads, exhibiting a higher diversity rather in other tribes and the same is true of the pollinia and this associated structures. Among the stapeliads the shape and surface textures of the corolla have diversified to a remarkable degree, and the two series of corona lobes also exhibit an extraordinary diversity.

Fruit, seed and seedlings

In the asclepiads, after fertilisation the flower falls off and the sepals close up tightly around the fertilised ovaries. In no-succulent genera where the flowering stems are ephemeral, fruit develops from this 'fertilised pedicel' without much delay and the same is true even in highly succulent-stemmed species of *Ceropegia* such as *C. dimorpha*.

However, in the stapeliads an important innovation has arisen: the ability of these 'fertilised pedicels' to remain in this state for long periods before developing into a fruit.

My own experience is that in some cases the development of fruit may be retarded for up to four years after fertilisation. Such a form of staggered production of fruit is unknown in any other succulent plants and it is clearly an important factor in assisting the relatively briefly viable seed to germinate at a suitable time or to spread the release of seed generated by a year of good flowering over several subsequent seasons. This phenomenon was first observed in certain Namibian stapeliads by Dinter (White & Sloane 1937: 6) and has since been observed in *Duvalia*, some species of *Orbea*, *Caralluma tuberculata* (Meve 1997) and in *Pseudolithos* (Bally *et al.* 1975). It is also common in *Quaqua*, *Hoodia* and *Larriyleachia* in southern Africa and in the thick-stemmed species of *Caralluma* in north-western Africa. Delays of up to a year in the development of fruit have also been observed in *Frerea* in cultivation. It is unknown whether this delayed development occurs in any of the slender-stemmed species of *Caralluma*, where the flowering stem often die back in the dry season. Amongst other asclepiads, similar inhibition of the development of fruit has been reported in *Sacostemma viminale* in Australia (Howie 1991).

In the stapeliads the fruit consists of a pair of slender, horn-like follicles (fig. 36). In most species the two horns are held at an angle of between 30° and 60° to one another. In *Ceropegia* many species produce them at between 150° and 180° to each other and this is found in a few stapeliad genera as well, especially *Pseudolithos*, some species of *Caralluma*, some *Larriyleachia* (fig. 36 C) and in some *Tromotriche*. This phenomenon is found especially in species that grow in very exposed positions where the plant itself or a surrounding bush is unable to protect the follicles from damage.

The follicles are mainly slender (3-5 mm thick), tapering gradually to a fine tip, but in a few species (such as *Tridentea pachyrrhiza*, *T. peculiaris* and *Whitesloanea crassa*) they are up to 15 mm thick and only 40-60 mm long. The smallest follicles observed were in *Ophionella willowmorensis* and *Baynesia lophophora*, where they are only 15-30 mm long. Follicles can reach a length of 200 mm in *Orbea distincta* from Tanzania and Kenya and these are the largest seen. Seeds are always stored in several rows inside (fig. 37), unlike in *Ceropegia*, where there is sometimes a single row along the follicle. They may be present in small to quite impressive numbers. A single follicle in *Ophionella willowmorensis* may have as few as 10-15 seeds in it whereas a pair of follicles in *Stapelia pillansii* was recorded with 691 seeds. In many species the outside of the follicle is smooth but longitudinally marked with dark purple lines. In *Stapelia* the follicles are finely pubescent outside and they are somewhat rugulose in some *Stapelianthus*. However, none

of the strange excrescences found on the fruits in *Marsdenia*, *Gomphocarpus* or *Pachycarpus* are known in the stapeliads.

In southern Africa seeds of stapeliads mainly ripen in the months of November and December, i.e. during the onset of summer and when the first rains begin to fall in the summer-rainfall regions. This is irrespective of when the plants flower.

When it is ripe, the follicle splits longitudinally along a suture on its ad axial (ventral) surface and releases the seeds (fig. 38). Each seed has a cluster (usually known as a 'coma') of fine transparent hairs 10-25 mm long attached at its micropylar end. On release from the follicle, these hairs spread out like a parachute and enable the seeds to disperse on whatever wind there is. Many of them land up under or entangled in nearby shrubs, after which the seed soon falls off from the coma and becomes buried in leaf-litter under the bush. Seeds of stapeliads are certainly also able to disperse over long distances. In the drier areas of southern Africa they are especially helped along by the frequent local whirlwinds or 'dust-devils', which may be powerful enough to lift loose bushes hundreds of meters into the air and dump them many kilometers away. Direct evidence for this ability to disperse over distance is seen in the appearance of seedlings of *Araijia sericifera* and *Cynanchum obtusifolium* in gardens in Cape Town and this phenomenon was also reported by Jonkers (1990) in parts of Arabia.

Seeds of stapeliads vary from about 2 mm long in some *Pseudolithos* to 10-12 mm long in *Frerea indica*, while most are 4-7 mm long and 2-4 mm broad. In southern Africa unusually large seeds are found in some species of *Orbea* such as *O. longidens*, where they may reach 10mm long and 6 mm broad. The seeds are flat to boat-shaped (i.e. somewhat longitudinally folded towards the ventral side) and they are usually pear-shaped to elliptical in outline, with the coma attachment to the narrower end (fig. 39 A-D). Around their edge there is always a distinct margin which is much swollen on the ventral side and not at all developed on the dorsal side of the seed (Sylla & Albers 1989). Such swollen margins are also commonly found in *Brachystelma* and *Ceropegia* and they consist of tall, empty cells with unusually punctured walls between them and, sometimes, attractively sculptured outer walls (fig. 39 E-H). Seeds are generally brown, sometimes reddish and often the margin is distinctly paler than the rest of the seed. The entire surface is papillate in *Notechidnopsis*, *Pectinaria* and *Quaqua*, where the margin also has the same colour as the rest of the seed. In most others the surface is fairly smooth. Hairs rarely continue along the margin away from the micropylar end and this is known in the stapeliads only in *Larriyleachia marlothii* (fig. 39 B). There are a few other

(Left) Fig. 41. Seedlings (half to one month old) of *Ceropegieae*. r = radical, h = hypocotyl, c = cotyledon, s = young shoot (these are only shown in A and E). Cotyledons leaf-like, hypocotyl absent to slightly succulent. A, *Brachystelma* c.f. *caudatum* (PVB 3708), cotyledons with long petioles. B, *Ceropegia nilotica* (PVB 4460), hypocotyl cylindrical. D, *Frerea indica* (PVB 5925), hypocotyl slightly wedge-shaped. Hypocotyl wedge-shaped, cotyledons reduced. E, *Orbea longidens* (PVB 4449). F, *Hoodia pedicellata* (Swakopmund, E. Erb). Hypocotyl wedge-shaped, cotyledons ± absent. C, *C. stapeliiformis* (PVB 6307). G, *H. pilifera* subsp. *pilifera* (PVB 4201). H, *Ophionella arcuata* subsp. *mirkinii* (PVB 4257). I, *Huernia verekeri* subsp. *verekeri* (PVB 4125). Scale bars: A, 5 mm; B-G, H, 2 mm (at D); I, 3 mm.

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Genus	Number of species	Number of species for which counts exist	Number of species with 2n = 22	Species with 2n = 22 or 44	Species with 2n = 44	Species with 2n = 66 or higher
<i>Anomalluma</i>	2	1	1	—	—	—
<i>Australuma</i>	2	2	1	<i>A. ubomboensis</i>	—	—
<i>Ballyanthus</i>	1	1	1	—	—	—
<i>Baynesia</i>	1	—	—	—	—	—
<i>Caralluma</i>	47	45	41	<i>C. adscendens</i> , <i>C. edulis</i>	—	<i>C. burchardii</i> (Canaries: 2n = 110-141 Morocco: 2n = 66), <i>C. joannis</i> (2n = 66)
<i>Duvalia</i>	14	14	9	<i>D. polita</i> , <i>D. sulcata</i>	<i>D. caespitosa</i>	<i>D. corderoyi</i> , <i>D. immaculata</i> (2n = 66)
<i>Duvaliandra</i>	1	1	1	—	—	—
<i>Echidnopsis</i>	21	19	14	<i>E. malum</i> , <i>E. scutellata</i> , <i>E. squamulata</i>	<i>E. seibanica</i> , <i>E. watsonii</i>	—
<i>Edithcolea</i>	1	1	1	—	—	—
<i>Frerea</i>	1	1	—	—	<i>F. indica</i>	—
<i>Hoodia</i>	14	10	10	—	—	—
<i>Huernia</i>	49	43	33	<i>H. aspera</i> , <i>H. hilsopii</i> , <i>H. kenensis</i> , <i>H. lodarensis</i> , <i>H. volkartii</i>	<i>H. erinacea</i> , <i>H. procumbens</i> , <i>H. recondita</i> , <i>H. archeri</i>	<i>H. leachii</i> (2n = 66)
<i>Larryleachia</i>	5	4	4	—	—	—
<i>Lavrania</i>	1	1	1	—	—	—
<i>Notechidnopsis</i>	1	1	1	—	—	—
<i>Ophioneia</i>	2	2	2	—	—	—
<i>Orbea</i>	56	50	38	<i>O. gerstneri</i> , <i>O. maculata</i> , <i>O. variegata</i> , <i>O. woodii</i>	<i>O. ciliata</i> , <i>O. macklooghlinii</i> , <i>O. melanantha</i> , <i>O. longidens</i> , <i>O. paradoxa</i> , <i>O. semota</i> , <i>O. speciosa</i> , <i>O. vibratilis</i>	—
<i>Pectinaria</i>	3	3	3	—	—	—
<i>Piuranthus</i>	7	7	7	—	—	—
<i>Pseudolithos</i>	4	2	2	—	—	—
<i>Quasqua</i>	19	16	16	—	—	—
<i>Rhytidocaulon</i>	11	4	4	—	—	—
<i>Richtersveldia</i>	1	1	1	—	—	—
<i>Socotrella</i>	1	0	0	—	—	—
<i>Stapelia</i>	29	26	22	<i>S. hirsuta</i> , <i>S. pearsonii</i> , <i>S. schinzii</i>	<i>S. engleriana</i>	—
<i>Stapelanthus</i>	6	6	5	<i>S. decaryi</i>	—	—
<i>Stapelopsis</i>	8	8	7	—	—	—
<i>Tavaresia</i>	2	2	2	—	—	—
<i>Tridentea</i>	8	8	7	<i>T. peculiaris</i>	—	—
<i>Throtriche</i>	9	9	7	<i>T. thudichumii</i>	—	<i>T. revoluta</i> (2n = 66)
<i>Whitesideana</i>	1	1	1	—	—	—
Total species	328	288	242 (74%)	23 (7%)	17 (6%)	6 (2%)

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Asclepiads where they continue right around the edge of the seed (*Fockea sinuata*, some species of *Hoya* and *Raphionacme namibiana* of the Periplocoideae).

Germination of the seed takes place with the radicle breaking through the seed coat (or testa) on the dorsal surface near the margin and not through the micropylar region, which is hardened by the production of the hairs of the coma (Meve 1997).

Inside the seed there is a comparatively large embryo (fig. 40). Within the *Ceropegieae* one many trace a definite increase in succulence in this structure with the progressive reduction of the cotyledons and with the acquisition of an increasingly succulent hypocotyl until the situation typical of many stapeliads is reached. It is interesting to observe that within *Ceropegia* the same development can be found, so that the embryo and newly germinated seedling of *C. stapeliiformis* is similar to that in many Stapeliads. The increased succulence of the hypocotyl and the reduction of the cotyledons in the embryo are even more obvious in the seedling; a selection of these is shown in fig. 41. It is particularly noteworthy that this reduction is quite obvious within several genera as, for example, in *Hoodia* (fig. 41 F, G), *Orbea* and *Tridentea* (Bruyns 1995a). Also it is often the case that, in a particular genus, the species with the most reduced cotyledons inhabit the winter-rainfall region to the west of the subcontinent and those with the larger cotyledons are found further north-eastward into the summer-rainfall areas. In general, there is a rough correlation between the size of the cotyledons and the size of the subsequent leaf-rudiments.

The increasing succulence of the newly germinated seedling with photosynthetic hypocotyl is important in helping the new plant to weather periods of irregular and unreliable rainfall during the crucial period in this life from germination to firm establishment as a plantlet (Von Willert *et al.* 1992: 51) and must have played a major role in the success of the stapeliads in the arid areas. A similar increase in succulence in response to aridity is found in *Ceropegia* but, despite this, *Ceropegia* has not radiated as successfully into the more arid parts of southern Africa.

to $x = 6$ in the Echiteae (Endress & Bruyns 2000) among some apocynacs, among the asclepiads it has only been recorded as low as $x = 9$ (Albers *et al.* 1993). Since this is found among members of the tribe Asclepiadeae, this lends support to the hypothesis that $x = 11$ is basic to the subfamily Asclepiadoideae, as it is to the Apocynaceae as a whole.

Chromosome counts (table 3) have been done for many species of stapeliad since a few were first recorded by the Italian botanist P. Pardi in 1933. Some earlier numbers given have proved to be incorrect but with a more careful approach towards the determination of the plants and the deposition of voucher specimens this has generally improved. Nevertheless, identification of material remains problematic and, for example, no explanation has been offered for the fact that *Tromotriche revoluta* has been given as having $2n = 44$ (Albers & Austmann 1987), $2n = 66$ (Albers & Delfs 1983) and $2n = 22 + 2B$ (Albers & Meve 2001)! The published results (as per references given in Albers & Meve 1991; 2001) have shown that 74% of all stapeliads are exclusively diploid ($2n = 22$), 6% are exclusively tetraploid while only 2% have $2n = 66$ or higher (see table 3). This 2% is made up of six taxa of which two are found in the arid coastal parts of Morocco in North Africa and the remaining four are found in southern Africa, if one includes *Huernia leachii* from central Moçambique and Malawi. Among the genera, chromosome numbers higher than $2n = 22$ have been observed in 36% of all species of *Duvalia*, which is the genus with the highest percentage of polyploids among the stapeliads, followed by 27% in *Orbea*.

Chromosome numbers

The combination of morphological characters and chromosome numbers has proved useful in the classification of many families and in some cases even the morphology and behavior of the chromosomes themselves have been useful as indicators of relationships (Raven 1975).

In the Apocynaceae in the broad sense this has not been the case since the family is cytologically quite uniform. In the Apocynaceae the basic chromosome number is assumed to be $x = 11$ (Raven 1975) and, while this descends

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Flowering times

In the systematic account, flowering times are not given for the individual species since it has been found that they are extremely variable.

If plants are cultivated under conditions of regular watering more or less throughout the year ten certain flowering times are indeed adhered to. In the southern hemisphere under these conditions, by far the majority of species flowers as autumn begins, i.e. from February onwards, with a peak during the months of March and April, after which flowering becomes more sporadic and usually ceases altogether after May. Nevertheless, throughout the summer months flowers appear, especially on the species of *Duvalia* and *Huernia*, on some forms of *Piarranthus geminatus* (whereas the other species of *Piarranthus* all flower later in autumn) and on specimens of *Stapelia hirsuta* var. *baylissii*, var. *tsomoensis*, var. *vetula* and *S. obducta*. There are certain species that flower in spring and these include the three species of *Pectinaria*, *Quaqua aurea*, *Q. cincta*, *Q. incarnata*, *Q. linearis*, *Q. marlothii* and *S. rufa*.

In the field, rainfall is often extremely erratic and there may be long periods where no rainfall is received at all, during which time plants can become extremely desiccated. If sufficient rainfall is then received anytime between spring and autumn (but even sometimes in winter) after such a dry period, plants quickly swell up (within 1-3 days) and, as soon as new growth starts to appear, they may begin to flower. Thus, for example, after good rains in December 1988, of the 16 species located on the eastern flank of the Great Karas Mountains, all except *Hoodia flava* were found in flower in January 1989. On the other hand, after very little rain in the summer of 1992/3 in the same area, although most of the species were found again, none of them were flowering. Similarly, after some rain in November 1976 in the Lekkersing area of Namaqualand, *Stapeliopsis neronis* was seen in flower in December of that same year. Even in the relatively cool time of winter, flowers will develop and early in August 2000 many were seen, after much delayed winter rains, on *Orbea namaquensis* east of Springbok though, at the time, none of the other seven species noted in the vicinity were flowering. The phenomenon of opportunistic flowering is often observed for widespread species such as *Hoodia gordonii* where, about a month after good rains have been received, plants become covered with flowers. This makes them conspicuous in areas that one has often driven past at various times of the year and not noticed them at all. This ability to flower whenever circumstances are suitable, rather than at fixed times, is clearly significant in assisting these plants to survive in areas where rains are erratic.

Even under fairly dry conditions, there are many species that adhere quite strictly to their

autumn time of flowering, especially in and around the edges of the winter-rainfall region. So, quite shriveled specimens of *Piarranthus punctatus* have been seen flowering bravely in April and May in the Ceres Karoo long before any rains have appeared. This is true also of species such as *Quaqua mammillaris* and *Stapelia hirsuta* var. *hirsuta*, among others.

In most stapeliads the flowers tend to remain open for 2-4 days. The most fleetingly open flowers are those of *Piarranthus atrosanguineus*, which mainly close again within a period of at most 18 hours. In plants which produce dense clusters of simultaneously opening, relatively large and evil-smelling flowers, the flowers mostly do not last for longer than two days – as in *Orbea huillensis* and *O. lutea*. Flowers which have only a faint odor or no detectable odor seem to last the longest. I have known flowers of *Stapelia engleriana* (which produce only a faint bad odor) to last for as long as eight days and those of *Huernia barbata* (which appear to be odourless) may last for 7-8 days.

The mechanics of pollination in the Stapeliads and self-fertility

There are two processes that need to be understood here. The first is removal of pollen from the flower and the second is insertion of pollen on another flower.

A fly visiting the flower is encouraged to view the flower more closely by gradients in the scent. It has been found that scent is given off weakly by the corolla lobes but more strongly by the swollen mouth of the corolla tube or annulus (Jahnke 1989) and this may persuade the fly to concentrate its energies towards the centre of the flower. There it is likely to discover the small pools of nectar that lie about on the corona and near the base of the guide-rail. As the fly scurries around trying to mop up this nectar, hairs on its proboscis or on a leg may enter the base of the guide-rail. The horny margins of these rails are such that, if something becomes caught in them, pulling it upward and outward does not release it but causes it to run further upward in the rail. As the upper end of the rail is confluent with the slit in the corpuscle, the hair is then guided into this. This slit narrows upwards and so the hair is soon caught. If the fly, now not surprisingly becoming a bit alarmed, tries to free itself by pulling harder, the entire pollinarium might be dislodged. Flies that are too small and consequently not strong enough to free themselves may be martyred in this position; this has often been reported and has led to the incorrect notion that many Asclepiad flowers are insectivorous. At any rate, by this complicated procedure, pollen is removed from the flower. As indicated above, removal of pollen can be achieved artificially with a fine pair of tweezers and then the guiding system provided by the guide-rails is bypassed.

The transfer of pollen is an even more complicated and risky procedure.

A fly that has fallen victim to the above unpleasant experience and has successfully removed a pollinarium will initially try to dislodge the pollinarium from its proboscis. Even if it fails to unseat it, the fly will in all probability not have learnt from its late nasty encounter with the stapeliad flower and might be foolish enough to visit another. Pollination is effected as follows. In the fly's frenetic ramblings over the flower the lower end of the insertion-crest (i.e. that nearest the corpuscle) on one of the pollinia might connect with the base of the guide-rail. Any upward jerking movement tends to cause the rest of the insertion-crest to slip in behind the rail. Since the insertion-crest thickens above and the rail becomes slightly narrower towards the top, the pollinium becomes stuck towards the top of the rail, after which further jerking will break off the yoke (i.e. the caudicle) between the pollinium and the rest of the pollinarium, which still remains attached to the hapless fly. This leaves the pollinium adhering to the outside of the guide-rail (fig. 33), though held in it firmly by the insertion-crest that is lodged in the guide-rail, while the fly makes off with the remainder.

The small amounts of nectar that are produced behind the guide-rail stimulate the pollen grains to germinate. The pollen tubes grow out rapidly through the pore that opens at the insertion-crest (fig. 31 C, D) and pass into the style head just behind the guide-rail. In the stapeliads (though not in all asclepiads) part of the style head (known as a *comptum*) just above the narrow necks of the ovaries distributes the pollen tubes roughly equally between the two ovaries and causes both ovaries to be fertilised (Kunze 1991). It follows from all this that the receptive region on the style head (i.e. the part corresponding to the conventional 'stigma') is restricted to the five small patches on the side of the style head behind the guide-rails.

Pollination can be done artificially under a microscope with a fine pair of tweezers. For artificial pollination, it is usually essential to have two different flowering clones for success to be likely. Anyone trying to pollinate stapeliad flowers will immediately notice that the main difficulty lies in holding the pollinarium in such a way that an upward movement will drag the insertion-crest of one of the pollinia into the guide-rail. This correct orientation is hard to achieve in some cases but, once found, the pollinium goes into position extremely easily and breaks off from the remainder with no difficulty. It will soon also be noticed, if this procedure is tried, that holding the pollinarium by the corpuscle is not always successful – it is so hard that any pressure will often cause it and the whole pollinarium to shoot away and forever be lost. The best place to take a grip on the pollinarium appears to be on the wings of

the corpuscle, if that is possible. In some cases the difficulties involved, because of the small size of the pollinarium and the restricted space around the guide-rail, are considerable and one is led to wonder how any seeds are ever produced. Actually the flower is cunningly adapted to assist the insect to achieve all this. For one thing, the shape and position of the various corona lobes are critical in guiding the insect into a useful position. So, for example, the fin-like dorsal process often present on the inner lobes helps to compartmentalize the space around the gynostegium and concentrate the activities of a visitor closer to the base of the guide-rail. The same function is equally often taken on by the outer corona, especially where it forms a deep bay around the guide-rail. In addition, small puddles of nectar around the edge of the guide-rails, inside the rails and on the base of the outer corona lobes often assist. If a pollinium touches such a puddle, the puddle's surface tension may orient the pollinium so that it is in an excellent position to enter the rail; similarly, nectar within the rail may pull an already partly inserted pollinium further into the rail.

Self-fertility is comparatively rare among the stapeliads. This phenomenon has been observed in *Stapelia villetiae* (Leach 1985) and in several species of *Duvalia* (Bayer & Harold 1987). It has also been reported (Hammer, pers. comm. 2001) in *Pseudolithos migiurtinus* and *Stapeliopsis neronis* and is known in the few hexaploid species (see table 3).

Since stapeliads are rarely self-fertile and since the pollination mechanism is complex and fraught with the possibility of failure, it is important that pollinia removed from a flower are not inserted on the same flower. It appears that when the flower opens, it takes some time for the guide-rails to dilate fully. So, initially, while a hair of the visitor's proboscis might pass through the guide-rails and remove a pollinium, the insertion-crest on the pollinium will not be able to enter the guide-rail for pollination. Visits to a flower by a fly are mostly short, so it is unlikely that the fly will remain around until the guide-rails are fully open and therefore the pollinia are most likely to be inserted on a different flower.

Pollinators and attractants

Many different insect groups have been implicated in the pollination of flowers in the asclepiads. Thus, for example, Wanntorp (1974) found that in Ceylon, *Calotropis gigantea* was [pollinated exclusively by a large carpenter pee. Honey-bees, Hymenoptera wasps, hesperid butterflies, moths and Diptera flies have been observed visiting flowers of *Sarcostemma* (Liede & Whitehead 1991; Kunze & Liede 1991; Ollerton & Liede 1997) and many of these were also observed to carry off pollinaria. Day-flying



Fig. 42. Flies visiting a flower of *Stapelia grandiflora* var. *grandiflora* (PVB 6884, near Fort Beaufort), in cultivation in Cape Town.

moths and wasps have been observed visiting the greenish- to yellow-flowered *Microloma armatum* (pers. Ops.) and species of *Gonolobus* (Kunze 1999), while Pauw (1998) has shown that even sunbirds are able to remove pollinaria in the bright red-flowered *Microloma sagittatum*.

Little is known of pollinators in the Secamonoideae, the subfamily that is sister to the whole of the Asclepiadoideae. Nevertheless it has been observed around Cape Town that flowers of the forest-dwelling *Secamone alpini* give of a faint bad odour and so flies are probably involved here. This would correspond to the suggestion of Banziger (1991) that evil-smelling flowers are typically found in plants that occur in dense forests. However, dark places are generally not inhabited by a wide variety of insects (Vogel 1978: 391) and this might be why the ubiquitous flies are employed here.

In species such as *Marsdenia macrantha*, which belongs to the sister tribe of the Ceropegieae, the flowers are sweetly scented and cream-coloured. Consequently they may be pollinated by bees, moths or flies - that is, they have a wide spectrum of visitors, many of which could remove pollinaria. In the Ceropegieae the spectrum of visitors becomes more restricted and flowers that are visited by nothing but flies become typical. In *Brachystelma foetidum* the flower has an excrement-like odour and is pollinated by flies, probably the common house-fly or blow-flies. The pollinators in *Ceropegia* are very small flies (micro-diptera) and their visits have been extensively documented (Vogel 1961; Bayer 1978), although field studies are still lacking. In *Ceropegia* these minute flies are temporarily trapped within the flower after being

attracted by various scents. During this period of isolation in the flower, nectar secreted in the guide-rails combined with a window-like effect which increases the light in the base of the tube, concentrate their attention towards the gynostegium and bring them into contact with the pollinia (Vogel 1961). After a day or two they are released as the flower tips over and as restricting hairs in the tube lose turgor. They may then visit another flower with the pollinarium that might have been picked up.

Stapeliad flowers are nearly universally fly-pollinated (fig. 42; Leach 1985; 1988; Endress 1994: 319; Meve & Liede 1994b). The only purported exceptions to the fly-pollination syndrome in the stapeliads are *Piarranthus atrosanguineus* and *P. decipiens* where it has been said that 'various moths are the principal pollinators' (White & Sloane 1937; Plowes 1989: 89). Evidence for this proposition does not lie in observations of the pollinators but in the fact that the flowers open in the late afternoon and close in the first few hours of the morning. However, Agnew (1976) indicated that these are generally the most active times for the emission of odours by the flowers and for fly activity. In addition, since both of these species have fairly evil-smelling flowers and a dark corolla with paler corona, all these factors suggest that flies are involved here too (Meve & Liede 1994b). Consequently one may assume that all the stapeliads are fly-pollinated. Generally stapeliads grow under bushes and in many cases their flowers are also comparatively hidden away in fairly dark places so that one might argue that their pollination by flies represents a reversal. This reversal is of particular selective advantage to the group since most grown in semi-arid to arid areas, where extended droughts often seriously reduce the diversity of insects available for pollination. In such areas flies are present at all times of the year (Faegri & Van der Pijl 1979), even in very adverse conditions, and their diversity is high in many arid areas (Bowden 1978). It is interesting to note that pollination by flies does not appear to be significant in the tribes Fockeeae and Marsdenieae and seems to be rare in the Asclepiadeae too. Exceptions are most common in the New World group, the Gonolobeae of the Asclepiadeae, where the flowers are also often dark-coloured, often flat, have very complex corona structures and seem to be evil-smelling.

Stapeliads have a highly complex pollination apparatus. Nevertheless, certain species such as *Caralluma adscendens*, *C. edulis*, *C. tuberculata* and *Orbea decaisneana*, among others, are extremely widely distributed. In addition, seed can be dispersed over a wide area and so plants run the risk of landing up in areas where there is no suitable pollinator. However, several examples are known where species have been taken well outside their area of natural occurrence but are still pollinated.

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One such case is the minute-flowered *Ophi-onella willowmorensis*, which has a restricted distribution in the arid mountains about 400 km east of Cape Town but is regularly pollinated in the greenhouse in Cape Town. A more extreme example is provided by the recently described *Baynesia lophophora* which, despite the small flowers with unusually shaped pollinia and the fact that its natural habitat is over 2000 km away has been pollinated each year here in Cape Town. Such cases are also found in the closely related genus *Ceropegia*, where a well-documented example is provided by *C. ampliata*. This species is widely distributed (South Africa to Kenya and Madagascar) but was still visited by insects and able to set seed in the Karoo Garden at Worcester which is around 400 km from its nearest known locality (Bayer 1978).

These various phenomena are explained by one or both of the following possibilities:

- (a) the pollinators are widely distributed species. Since flies exhibit a considerable ability to disperse (Bowden 1978), this factor may be quite significant;
- (b) pollination depends on the size of the fly and not on specific details of its shape, so that more or less any fly of the 'correct size' can 'do the job'.

Since one frequently finds several species of stapeliad growing socially and, since naturally occurring hybrids are scarce, it is probable that pollinator pressures have also contributed to speciation in the group. Different flowering times are found in such sympatric taxa as *Quaqua incarnata* (or *Q. aurea*) and *Q. mam-millaris* so that they may flower when entirely different types of flies are active (they emit, in addition, very different scents). Different scents are emitted by such sympatric taxa as *Q. pruinosa* and *Q. mam-millaris*, which flower at roughly the same time, so that these two probably attract different types of flies. Perhaps most significant are differences in the sizes of the pollinaria. Although smaller pollinaria than those of a particular species will readily fit into the guide-rails of that species, they will often slip right through the rails and may not be trapped. A good example of this is provided by the frequently sympatric *Stapelia kwebensis* and *S. schinzii*, which have pollinia of markedly different sizes. Both species have evil-smelling flowers and seem to attract similar flies to their flowers, but there is only one recorded case of a hybrid between them (Giess 1974). A similar scenario is provided by *S. hirsuta* and *S. panicu-lata*, where no hybrids have ever been discovered. These pairs of species appear to have evolved to use the same pollinator and flower at the same time, often near to one another.

In all stapeliads the attraction of flies appears to take place by the flower imitating their feeding or breeding substrate. This is achieved in two ways.

- (1) The emission of an odour suggestive of this substrate

In the stapeliads a wide range of odours is involved. Obviously the most striking and memorable are those that have evil odours of excrement, urine or rotting flesh. These are found particularly in the larger-flowered species but, very roughly, it can be said that, apart from their presence in certain (generally larger-flowered) species of *Caralluma*, *Hoodia*, *Larryleachia* and *Quaqua*, they are found mainly in the genera with few-flowered, solitary inflorescences (*Duvalia*, *Orbea*, *Stapelia*, *Tavaresia*, *Tridentea* etc.) and in *Edithcolea grandis*. These bad odours are particularly attractive to larger flies such as members of *Calliphora*, *Musca* and *Sarcophaga*, and generally the flowers involved have larger pollinaria which need a larger fly to shift them. It is interesting to note that all the large-flowered species have evil-smelling flowers and this is especially true of the very large flowers in *Hoodia* and *Stapelia*. As mentioned above, the flowers of *Stapelia gigantea* are among the largest of all known flowers. What is remarkable is that plants with larger flowers, such as certain species of *Aristolochia* and *Rafflesia* (where the flowers reach 1 m in diameter and are the largest known among the flowering plants) are all evil-smelling and pollinated by flies. The same is true of many members of the *Arum* family, where the inflorescences are especially large (e.g. *Amorphophallus*). It is also curious that the flowers in *Rafflesia* have a similar shape to that of species such as *Orbea namaquensis*.

Less striking odours are also common. Odours resembling sweat and rotting or over-ripe fruit have been observed and pleasantly sweet, honey-like, lemon-like or mango-like odours are also known. A fairly strong and distinctly mushroom-like odour has been observed on the tiny flowers of *Echidnopsis dammanniana* from Ethiopia and Kenya. Among genera with mostly large-flowered species, unusual odours are sometimes found in smaller-flowered species but are exceptional (e.g. *Orbea schweinfurthii* and *Stapelia flavopurpurea*). In *S. flavopurpurea* the odour varies from sweet to bad. A sweet odour is emitted by greenish to yellow flowers, while brownish to reddish flowers may be more evil-smelling. In some cases these still attract larger flies but in general it appears that much smaller ones of the *Drosophilidae* (fruit-flies) and *Milichiidae* are attracted, and Agnew (1976) found that only *drosophilids* were attracted to flowers of *O. schweinfurthii*. In these small-flowered species the pollinaria are small and may be removed readily by small flies.

- (2) The resemblance of the colour and texture of the corolla's inner surface to this substrate

This is achieved by various patterns of striking to somber colour or a mainly dark colour. It has been shown that these patterns alone have no attractive value but, when combined with the odour of decayed protein, they are very effective in luring flies to a flower (Faegri & Van der Pijl 1979). In addition, the surface is often convoluted with ridges or papillae. In the largest-flowered species of *Stapelia* these papillae take the form of fine hairs. The combination of an evil smell, the brownish colour and these hairs, which altogether possibly resembles the fur of a dead animal stimulates blow-flies to deposit their eggs on the corolla. This peculiar phenomenon is well known in large-flowered species of *Stapelia* (e.g. *S. gettiffei*, *S. gigantea*, *S. grandiflora*, *S. hirsuta*, *S. schinzii* and *S. clavicorona*) in southern Africa and also occurs in *Edithcolea grandis* in north-east Africa. This phenomenon was first recorded by Compton (1934) in *S. schinzii*. Tiny flies have also been observed to lay their eggs among the hairs around the base of the corolla tube in *Stapeliopsis neronis*. Egg laying by flies has never been observed in those flowers producing less foetid odours (Agnew 1976; own obs.). Since the larvae hatch but are unable to survive, this wastage of eggs is counter-productive to the fly. As a consequence, Agnew (1976) suggested that pollination of large-flowered stapeliads by blow-flies is a more recent development.

Additional attractants are provided by:

- (1) Vibratile cilia along the margins of the lobes

These move in the slightest breeze and might imitate the movement of other flies (or their wings) which are already present on the flower. These cilia may exploit the tendency of flies to be optically attracted by moving objects or it may be that their movement appeals to the gregarious instincts of flies (Vogel 1961: 183; Faegri & Van der Pijl 1979). They are found in many unrelated genera in the stapeliads and are also common in *Ceropegia* but are somewhat less frequent in *Brachystelma*.

- (2) The secretion of nectar

Nectarial secretions are always present behind the guide-rails, where a bank of secretory cells is located, and some of this secretion is required to stimulate the growth of pollen tubes in an inserted pollinium (Kunze 1995a). Excess nectar tends to run down from the rails and collect within the cavity formed by the outer corona.

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Nectanal secretions are also often present on the corona, where shiny pools of lequid are formed. These were first noticed by N.E. Brown (1902-03) in *Piранthus decipiens* but have since been observed in many other species (e.g. Bruyns 1986a for *Orbea miscella*; Meve 1994 for various species of *Piранthus*).

Within the stapeliads, four different basic adaptations to or strategies for fly pollination (fig. 43) may be identified.

(1) Open-access flowers

These are flat to campanulate flowers where the fly can alight freely, has ready access to the pollinia and nectar, and can leave again when it pleases. They are by far the most common in the stapeliads. They exhibit enormous variation in size within the group, and may be 200-400 mm in diameter in *Stapelia gigantea* (Leach 1985) and only 6 mm in diameter in *Laryleachia cactiformis* (Bruyns 1993). In both cases, frequent visitors are the common house-fly and blow-flies (Meve & Liede 1994b).

(2) Trap flowers

A simplified form of the trap-mechanism which is operative in *Ceropegia* and was outlined briefly above also seems to be found in a few stapeliads. This is particularly the case in the five species of *Stapeliopsis* other than *S. pillansii*, and in *Echidnopsis malum*. In *S. exasperata*, *S. khamiesbergensis*, *S. neronis* and *S. urniflora* the mouth of the tube is the limiting factor and in the last three it is extremely narrow. In *S. breviloba*, *S. saxatilis* and *E. malum* the lobes remain joined at their tips at anthesis and it is the gaps between them which are narrow and restrict access to the flower. Very tiny flies seem to enter the flower. The interior is ornamented with papillae and hairs and the hairs become longer towards the base of the tube. This forces the insect to concentrate its activities towards the gynostegium in the centre. The impression has been created repeatedly that these tiny flies become trapped within the flower, a phenomenon first reported for *S. breviloba* and *S. neronis* (Bruyns 1979). It is likely that the flies leave the flower once it begins to shrivel and the hairs on the corolla tube lose turgor.

(3) Fungus-gnat flowers

There are a few stapeliads in which the flower is a narrowly cylindrical or urceolate stricture, the mouth of which is placed close to the surface of the ground, sometimes even slightly buried in loose leaf-litter. Such flowers are known in *Echidnopsis ballyi*, *E. mijerteina* and *Stapeliopsis exasperata*. Another case is presented by *S. pillansii*, where the flowers mature beneath the surface of the ground. Here plants observed in habitat were found to have their flowers embedded in soil made very loose by the activity of ants (M.B. Bayer, pers. comm.) which could have facilitated the movement of small flies in the cracks and cavities underground. Similar flowers to those of *E. mijerteina* are found in *Brachystelma campanulatum*, *B. gymnopodium* and *B. oianthum*.

It is not at all clear how these flowers are pollinated. Flowers maturing underground are known in some Australian orchids and very small flies have been found carrying the pollinia in one of these (Clements & Cribb 1984). Some small-flowered aroids have been found to be visited by



Fig. 43. Different adaptation to fly-pollination in flowers of stapeliads. **A**, open-access flower for *Stapelia kwebensis* (PVB 5541). The flower is roughly 25 mm in diameter. **B**, trap-flower of *Stapeliopsis breviloba* (PVB 1704). Each flower is about 12 mm long. **C**, possible fungus-gnat-flower in *Echidnopsis mijerteina* (Carter 23385). The flower is about 20 mm long. **D**, possible exclusion-flower in *Pseudolithos caput-viperae* (hort.). The flower is 2,5 mm in diameter.

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fungus-gnats (Vogel 1978; Boyce 1993) and it is possible that similar gnats are involved here, especially since in some of these species the pollinaria are extremely small. In *Echidnopsis mijerteina* the inside of the corolla is even highly convoluted, as is often the case in such flowers (Vogel 1978).

(4) Exclusion flowers

There are several asclepiads where the pollinator is expressly prevented from entering the flower. Removal and insertion of pollinia is achieved by the careful directing of a probing proboscis by outgrowths of the corolla, by the corona or even by outgrowths of the anther. Such flowers are known in *Microloma* (Bruyns & Linder 1991) and in *Dischidia* (Rintz 1980). In both cases, the blocking of the mouth of the corolla by hairs or by the lobes themselves prevents smaller insects, which would be unable to move the pollinaria, from entering.

It seems possible that the flowers in some species of *Sisyranthus* function in the same way and there is evidence to suggest that the same syndrome is also found in *Pseudolithos*, especially in *P. caput-viperae*. In this species the opening to the flower is less than 1 mm across and the corona and much of the tube are nearly filled with nectar. In addition, the relatively large and sturdy corpuscle on each pollinarium suggests that it is built to withstand 'rough treatment' and is not removed by a very small fly. Hairs are also present on the inside of the corona to force a slender, probing organ towards the guide-rails. This is the only such case known among the stapeliads.

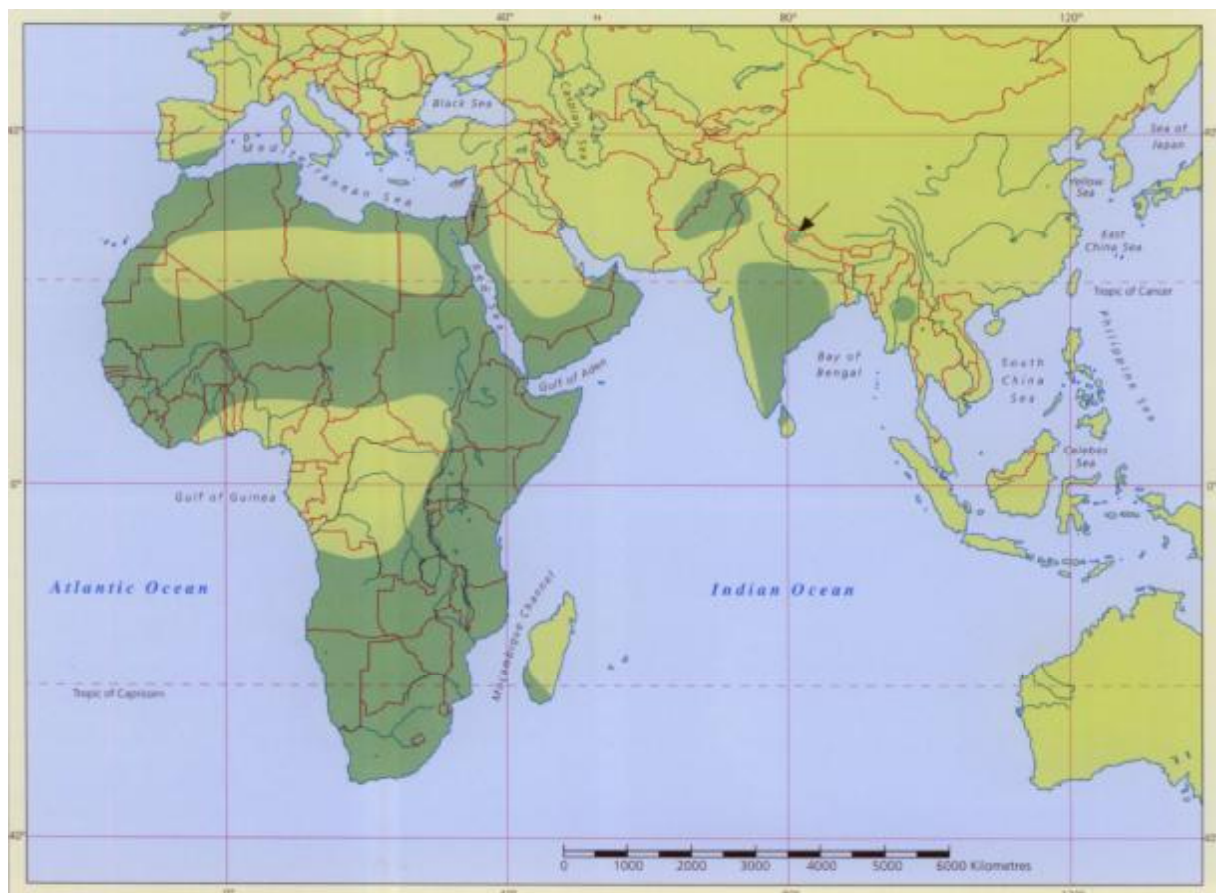


Fig. 44. World-wide distribution of the stapeliads

Biogeography of the Stapeliads

Patterns of Distribution and Diversity

Aspects of overall distribution of the stapeliads

Stapeliads are succulents and therefore they are found particularly in semi-arid to arid areas. Within the true deserts they are rare. Nevertheless, even here they do occur. So, for example, in a spot about 30 km from the coast and 150 km south of the Kunene River on the 'Skeleton Coast' of the Namib Desert, where less than 50 mm of rain falls annually, *Hoodia currorii*, *Huernia oculata*, *Larylechia marlothii*, *L. tirasmontana* and *Orbea maculata* subsp. *rangeana* were all found. On the other hand *Orbea variegata* flourishes on the slopes of Table Mountain at Cape Town, where it receives between 600 and 1 000 mm of rain annually, and stapeliads are found in parts of Moçambique where the annual rainfall exceeds 1400 mm (Jackson 1961). So extreme aridity is not essential for their survival.

In Africa two main centres of diversity for the stapeliads have been identified (Bruyns 2000b). The 'southern centre' lies in the tropical and temperate parts of southern Africa and is centred on Namibia and South Africa. The 'north-eastern centre', which is exclusively tropical, includes Ethiopia, Kenya and Somalia, together with the neighbouring parts of south-western Arabia. Three additional minor centres exist, in West Africa, in Madagascar and another in India, Myanmar and Nepal.

In the stapeliads we are dealing with 31 genera encompassing 328 species. These species are distributed through the Old World as indicated in table 2. Of these 31 genera, one is endemic to Madagascar and one to India. Nine genera are endemic to the north-eastern centre. On the other hand, 15 genera are restricted to the southern centre. At species level (not considering endemics only), Madagascar has six species, all of which are endemic; the Indian region has 15, of which 12 are endemic; the north-eastern centre has 119; and the southern centre has 182. There is therefore a considerably larger concentration at both the generic and specific levels in the southern centre (table 2).

Three genera have a pan-African distribution with species in both centres. These are *Duvalia*, *Huernia* and *Orbea*. Of these, both *Duvalia* and *Huernia* have far more species in southern Africa than in the north-eastern centre but in *Orbea* there are only slightly more in the south than in the north. In *Duvalia* there is one partial area in the north-eastern centre on both sides of the Red Sea. In *Huernia* and *Orbea* the position is more complicated as they are very much more widespread in the north-eastern centre than *Duvalia* and both have a third partial region in West Africa. In *Huernia* this consists of a single, small area but in *Orbea* there are several, apparently disjunct patches scattered

across the Sahara (mainly in the higher mountains) and species are also found along the coast between Senegal and Morocco.

The present-day distribution of the stapeliads (fig. 44, see also table 2) was previously explained as dispersal westwards from a place of origin in western India because of the presence in this area of the 'most primitive' stapeliad *Frerea indica* (White & Sloane 1937; Good 1953). However, this now seems an unlikely scenario.

It is now generally accepted that peninsular India formed part of Gondwanaland and broke away from it about 65-100 million years ago, i.e. during the Cretaceous (Axelrod & Raven 1978). According to the fossil record, the angiosperms were well established and underwent major evolutionary radiation during the period 130-90 million years ago (Crane et al. 1995). Nevertheless, the fossil record for the asclepiads is scanty, with leaves of *Cynan-cum*-like and *Vincetoxicum*-like plant known from the mid-Eocene (39-49 million years ago) in North America (MacGinitie 1933; 1941) and fossil pollen similar to that known in the present-day Secamonoideae recorded from Central Europe for the same period (Konzalova 1981). Consequently, it remains unknown whether stapeliads were actually present when Gondwanaland began to split up.

Speculation based on the present-day distribution of these plants suggests the following. From the fact that *Caralluma adscendens* is found in the north-eastern centre and in southern India and that another southern Indian species, *C. umbellata*, shows similarities to *C. acutangula*, which is widespread in sub-Saharan Africa, it seems possible that these species or similar elements were already present around the time of the break-up of Gondwanaland. One may be tempted to infer that the leaf-bearing genus *Frerea* is a relictual element which shares many features with a hypothetical ancestral stapeliad that occurred around the Horn of Africa and which managed to persist in a restricted niche of the higher mountains of western India (Tetali et al. 1997) after India moved away from mainland Africa. However, molecular analyses (Meve & Liede 2002) suggest that this is not the case, since *Frerea* is nestled among other stapeliads without conspicuous leaves.

Some of the molecular results suggest that the stapeliads originated somewhere in north-eastern Africa. From this region of origin in north-eastern Africa there seem to have been several major events of diversification in the stapeliads:

- (1) radiation into Myanmar, India and Nepal, where the species seem to consist of three elements. Firstly, there are those that were possibly present around the break-up of Gondwanaland and were 'rafted' to their present position. Secondly, there

are elements which occur only in the arid north-western part of the Indian subcontinent, extent westward into Pakistan, Afghanistan and Iran, and also occur widely in the Arabian peninsula (*C. edulis*, *C. tuberculata*). It appears that these have spread independently eastwards to India, as this type of disjunction is quite common in other groups (Thulin 1994). Finally, there are endemic elements that are unique to the Indian subcontinent.

- (2) radiation into West Africa, though the diversification has generally remained low there
- (3) radiation into Madagascar. Two schools of thought exist on where Madagascar originated. One is that between 165 and 121 million years ago it moved southwards from the coast of southern Somalia to its present position (Rabinowitz et al. 1983). Another is that it moved north-eastwards from the Moçambique coast and reached its present position around 60 million years ago (Flores 1970). The stapeliads of Madagascar are more closely allied to southern African taxa than to any occurring in north-eastern Africa (Bruyns & Klak, 2004). It is therefore possible that the relationships of the Madagascan stapeliads may lend some support to the latter theory. However, it is also possible that their presence in Madagascar was caused by a dispersal event which could have occurred even well after the separation of Madagascar from the African mainland. Dating techniques of molecular phylogenies could help to resolve this question.
- (4) radiation into southern Africa. Within southern Africa, diversification has proceeded from the summer-rainfall to the winter-rainfall parts exactly as was found by Gerbaulet (1992) and from the more mesic to the more arid parts. So here two factors appear to have driven speciation, namely changes in the rainfall regime and increasing aridification. It is also perhaps worthy of note here that speciation has been especially significant in mountainous areas where more niches and a greater diversity of soils are available. Changes in the timing of rainfall with the development of a winter-rainfall climate in the south-western corner of southern Africa may have occurred as recently as five million years ago (Axelrod & Raven 1978:112). The age of the aridification of the western part of southern Africa is the subject of much discussion. On the one hand there is considerable evidence that this region, and especially the Namib, has been arid to semi-arid since the Cretaceous of about 80 million years ago (Ward et al. 1983). This may suggest that the diversity in succulents that is found here has arisen over a long period, just as *fynbos* elements

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have been present for at least 60-70 million years (Scholz 1985).

On the other hand, the relatively recent origin of the Benguela Current (within the past 5-10 million years, Siesser 1980) is considered to have brought increasing aridity to the region (as well as greatly increased the aridity of the Namib). It may also have been responsible for changing the flora from lush and moist subtropical to tropical thicket 10-15 million years ago (Coetzee & Muller 1984) to semi-desert, as was documented for Langebaanweg for the past 5-10 million years (Hendey 1982). These changes are suspected of having brought with them the enormous diversification which is well known in the Cape Flora (Goldblatt & Manning 2000) and may equally well have brought about the remarkable diversity in the drier, adjacent Succulent Karoo. Our molecular data suggest that at least some of the diversity of stapeliads in north-eastern Africa (e.g. in the genera *Huernia* and *Orbea*) is due to migration northwards from southern Africa.

As pointed out above, there are three genera of stapeliad that occur in the arid areas of north-eastern Africa and south-western Africa. The existence of a north-eastern arid centre of diversity and a south-western arid centre of diversity on opposing sides of the African continent, which contain many closely allied taxa, has been noted in a wide range of plant groups (De Winter 1971; Gerbaulet 1992; Ihlenfeldt 1994; Thulin 1994; Jürgens 1997). However, recent taxonomic studies have shown that certain species, which were once thought to be vicariant between these two areas, actually consisted of two distinct species in the two regions (Thulin 1994). From among the stapeliads, De Winter (1971) suggested *Huernia insigniflora* and *H. somalica* and *Stapelia revoluta* and *S. prognatha* as examples of pairs of closely related species, where one occurs in the north-east and the other in the south-west. However, the latter two are not closely related at all (Bruyns 1995a; 2002) and there is no evidence that these two species of *Huernia* are particularly closely related either, despite their similar appearance (Leach 1988). Gerbaulet (1992) recorded a single species of *Anacampseros* L. common to southern Africa and Somalia (*A. rhodesica*), though Thulin (2002) has recently contested this view. Thus it appears that succulent genera which "occur in both areas do not have species common to both. This is the position in the stapeliads where, although there are three genera with species in both centres, only *Orbea schweinfurthii* is marginally common to both the north-eastern and southern centres, in the sense that its distribution stretches from the southern limit

of the north-eastern centre to the northern limit of the southern centre. This situation is not common to all families of plants and in *Acacia* (Fabaceae) there are two species common to both the north-eastern and the south-western centre (Ross 1979; Thulin 1994). In the case of the Pedaliaceae, Ihlenfeldt (1994) found that there were several genera with species in both centres but that only a single non-succulent species in the whole family (*Rogeria adenophylla*) is found in both centres.

Vicariance between north-eastern and southern Africa is known in other living organisms. Among the 284 species of mammals known in Africa, 27 species (10%) show a southern Africa/north-eastern Africa disjunction in their distribution. In several cases, such as the bat-eared fox, the black-backed jackal, the aardwolf and a species of *Oryx*, these taxa are restricted to the arid zones in these two regions and are entirely absent from the extensive *Brachystegia* / *Julbernardia* / *Colophospermum mopane* woodlands of central Africa (Coe & Skinner 1993). Among birds there are closely related species of sandgrouse in arid southern Africa and north-eastern Africa and, while their taxonomy is still somewhat confused, it remains clear that certain species of larks in north-eastern Africa are also closely related to others southern Africa (Clancey 1986). Among amphibians, it is known that there is one group of xeric species of *Bufo* (toads) which occurs in southern Africa as well as in the region from northern Tanzania to Somalia, with one species recorded in both areas. One species of frog (belonging to the genus *Tomopterna*) is widespread in Namibia and Somalia although its taxonomy in the south is not well clarified (Poynton 1995).

There is therefore considerable evidence of similarity in taxa (if not at the level of species, then among closely related species) between these centres of a wide range of living organisms. This similarity in taxa of plants between these centres was originally considered by Engler & Pax (1921) to be a consequence of long-distance dispersal. Despite the ability of stapeliad seed to move over considerable distances (Jonkers 1990), it is unlikely that long-distance dispersal is responsible for the presence of related species of stapeliads in the north-eastern and south-western centres especially since the species have diverged significantly within each of the genera common to the two centres. The fact that there is such disparity between the two centres at the level of species suggests that the separation into two centres is of considerable age and so the suggestion of Werger (1978) that in some senses an 'arid' corridor still exists today does not apply to the stapeliads. The absence of species of *Caralluma* closely related to *C. adscendens* in the southern hemisphere suggests that the 'arid corridor' joining the north-east of Africa

to the south-west (Verdcourt 1969; De Winter 1971; Werger 1978) was a relatively recent phenomenon in terms of stapeliad evolution or that it was never sufficiently dry for entirely free migration of stapeliads to have taken place. Much of the intervening territory between these two centres, especially in Malawi, Moçambique, Tanzania and Zambia, is covered by forest (or was until the forest was recently destroyed) in which species of *Brachystegia* dominate. It has been suggested (e.g. Gilbert 1990) that this *miombo* woodland is not conducive to the presence of stapeliads but this appears to be only partly true (see 'Sandy habitats' below).

It seems to be accepted that the whole of East Africa was considerably drier during the last ice age than it is now and that dry periods may have occurred before as well (Hamilton 1982). The presence of stapeliads in many quite isolated habitats in Malawi, Moçambique and southern Tanzania, where the relatively high rainfall (> 600 mm annually), the plentiful trees and dense, tall grass mostly prevents their growing at all, suggests that their distribution in these areas may have been much more extensive during former dry periods and that they have now 'retreated' to a few refugia where escape from dense grass growth and trees is still possible. Over much of the wetter parts of tropical and equatorial Africa, granite domes with skeletal soils provide the only 'arid refugia' and they are able to support a wide range of succulents under conditions of annual rainfall as high as 2 000 mm (Jackson 1961). Species of *Aloe* (Reynolds 1966) and *Euphorbia* (Leach 1976b) seem to occur widely on them. Some stapeliads grow on these inselbergs in Malawi, Moçambique, southern Tanzania, Zambia and Zimbabwe but they appear to be much less common on them than is the case for *Aloe* and *Euphorbia*. However, these are not the only places inhabited by stapeliads in these parts and they have, on many occasions, been found on the floor of *Brachystegia* forest where one or other factor has caused relatively local aridity. The highly mobile seed of the stapeliads makes them all the more able to 'find' such suitable spots, however widely scattered they may be.

The disjunction found between the north and south of Africa is somewhat different to the east/west situation within the continent. In the northern hemisphere there are several species with very broad distributions in an east/west direction. North of the Sahara *Caralluma europaea* is found along the margins of the Mediterranean, from Morocco and Spain to Jordan (Bruyns 1987b). In northern sub-Saharan Africa there are even more widely distributed species, some of which occur from the west coast of Africa to Somalia and south-western Arabia. The best examples are provided by *Caralluma adscendens* and *C. edulis*, both of which have especially wide distributions in an east/west direction and both of which are also found

in India (and Pakistan in the case of *C. edulis*, Bruyns 1989; 1992). Since both of these species are widely utilised, the extent to which man has contributed to these distributions is unknown but may be significant. Further examples are provided by *Caralluma acutangula* and *Orbea decaisneana*, which occur from West Africa to the north-eastern centre in Ethiopia, Somalia, Sudan and Arabia (Gilbert 1990; Thiede 1994). In Africa south of the Sahara there is physically no scope for such broad distributions. Nevertheless, again there are species that span the continent from west to east. The best examples are provided by *Huernia verekeri*, which is found from near the Atlantic in the Chela Mountains of south-western Angola to within a kilometer or so of the Indian Ocean in Moçambique, and *Stapelia kwebensis*, which is recorded from the Baynes Mountains of north-western Namibia to the Pafuri district in Moçambique.

Local levels of diversity of stapeliads outside southern Africa are difficult to estimate. Table 4 gives the numbers of species in the various genera that are known in Arabica and Socotra and in the countries that make up north-eastern Africa. From this it is clear that the highest number of species occurs in Somalia. It is also clear that outside southern Africa the diversity is mainly caused by the strong contribution of the genera *Caralluma* and *Echidnopsis*, with *Caralluma* making the largest contribution except in Socotra, where it is noticeably under-represented. Nevertheless, both the number of genera and the number of species are much lower than is found in South Africa. In parts of north-eastern Ethiopia the local diversity of stapeliads is remarkably high and 10 species were observed during a walk

which covered a distance of about 4 km to the north of Dire Dawa. The number may be a little higher in some parts of Somalia. The diversity of succulents in Somalia seems to be associated with a relatively low annual rainfall, some of which is received in winter, combined with skeletal soils derived from sand stone, limestone and gypsum (Lavranos 1971; Thulin 1994). The figures for local diversity seem to be generally lower in Arabia, although as many as 13 species have been recorded in the vicinity of Al Barh, west of Ta'izz in the former North Yemen in southern Arabia (Hanacek & Rikanek 2000). Further to the east, in India, as for example around Bangalore in Tamil Nadu, *Caralluma adscendens*, *C. indica*, *C. stalagmifera*, *C. truncata-coronata* and *C. umbellata* grow within about 5 km of each other. This is the maximum achieved anywhere on the Indian subcontinent.

Aspects of distribution of stapeliads in southern Africa

Of the 182 species recorded in southern Africa 167 (92%) are endemic. Here the major concentration of 152 species is found in South Africa (table 5) of which 63% are endemic. Namibia comes a somewhat pale second with 60 species with a much lower level of endemism (18%), despite the fact that it is the most arid country south of the Sahara (Seely and Jacobsen 1994). Far fewer species occur in the remaining countries on the mainland (i.e. excepting Madagascar) and in these countries there are only insignificant levels of endemism among the stapeliads.

In the southern centre, despite the relatively

comprehensive data on distribution, the true picture is far from revealed and the predictive value of Map 2 remains relatively low. So, for example, a recent sortie into the half-degree square 2716 B (using the notation of Edwards & Leistner 1971), where two species of stapeliad were known (Bruyns 2000b), revealed an additional eight species not previously found there. Many half-degree squares are empty of records, especially in the middle of South Africa and on the eastern flank of Namibia. In addition, Botswana, Zimbabwe and Moçambique are very poorly covered. In the case of the eastern side of Namibia and Botswana this is undoubtedly to due lack of collecting, since most of this area is eminently suitable for stapeliads, despite its low geological and topographical diversity. In Moçambique it appears that the position is different. Although again the records are not representative of the true position, investigations have shown that much of the country is inhospitable to stapeliads as it is too moist and is frequently covered with dense bush and tall grass.

In South Africa there are a few areas which are free of stapeliads. They are generally absent from the higher levels of the Cape Fold Mountains but this does not show up on the concentration maps since these peaks are interspersed with deep valleys and other more arid areas where they do occur. The all-year rainfall zone around George and Knysna also contains no stapeliads. Larger patches of countryside where they are absent are in the Drakensberg of Lesotho and the high-lying area to the north of this in the north-eastern Free State and southern Mpumalanga. Their absence here is caused by high rainfall and very low minimum tempera-

Table 4. The number of species in the genera of stapeliads in the countries north-east Africa, Arabica and Socotra.

Genus	Somalia	Ethiopia (+Eritrea)	Kenya	Sudan	Tanzania	Uganda	Arabia	Socotra
<i>Anomalluma</i>	1	—	—	—	—	—	1	—
<i>Baileyanthus</i>	1	—	—	—	—	—	—	—
<i>Caralluma</i>	14	13	11	5	4	5	15	1
<i>Duvalla</i>	3	1	—	1	—	—	2	—
<i>Duvallandra</i>	—	—	—	—	—	—	—	1
<i>Echidnopsis</i>	10	7	9	1	2	—	4	5
<i>Edithcolea</i>	1	1	1	—	1	—	1	1
<i>Huernia</i>	2	4	4	1	2	—	6	—
<i>Orbea</i>	4	9	8	5	5	3	6	—
<i>Pseudolithos</i>	4	1	—	—	—	—	—	—
<i>Rhytidocaulon</i>	4	2	1	—	—	—	6	—
<i>Socotrella</i>	—	—	—	—	—	—	—	1
<i>Whitesoana</i>	1	—	—	—	—	—	—	—
Total species per country	45	38	34	13	14	8	42	9

tures in the Drakensberg and by relatively deep soils and very heavy frosts in the area adjacent to this.

The number of genera per half-degree square (30' x 30') reaches a maximum of 11. The picture is very similar when numbers of species per half-degree square is examined (fig. 45) and the maximum recorded is 25 in one half-degree square. From the remarks above one can see that the level of diversity found in southern Africa is unique in the group.

These maps shown that in southern Africa the stapeliads are particularly concentrated towards the western and southern edges of the subcontinent at 28-34°S, i.e. well outside the tropics. Most of the highest diversity of genera and species occurs along the eastern edge of the winter-rainfall region near to the area receiving between 40% and 60% of its rainfall in winter. From 27°S these areas of highest diversity are found almost exactly along the escarpment, which runs roughly parallel to the coast. At around 32°S 21°E the escarpment swings eastwards and, while the concentrations of stapeliads along it remain higher than in nearby areas, they are much higher further south in the Little Karoo and

in the mountains bordering it (at around 33°S and 20-24°E). In particular localities (in an area of, say, 1-2 sq. km) it is not uncommon to find, after careful searching, six to eight or more stapeliad species growing more or less socially. The squares nearest to the coast always have lower concentrations than those slightly inland and this is particularly noticeable along the arid west coast. There is also a marked drop in the numbers in the south-western Cape, where the rainfall is higher. The central regions are very scantily covered, with an almost total absence from the Drakensberg and the high-lying region north of it. Towards the eastern side the covering is also generally less intense.

The area with the highest concentration of species per half-degree square is in the vicinity of Matjiesfontein (in the square 3320B) and here 25 species are found. Smaller localised centres of diversity occur in the Great Karas Mountains (18 species), the Pofadder/Warmbad district (12 species), in the region between Prieska and Kimberley in the Northern Cape (13 species), in the Soutpansberg and Blouberg (13 species) and in the upper mountainous reaches of the Olifants River (11 species) of Limpopo Province. Several other local peaks in distribution exist

as, for example, in the Baynes Mountains (8 species) and Tiras Mountains (14 species) of Namibia.

Among the stapeliads the variation in density of taxa is brought about by five factors:

- (1) Very localised species. In general this is a factor of low importance amongst the stapeliads, in stark contrast to the position in the succulent Aizoaceae. The wind-borne seeds are almost certainly responsible for this, as is well known in other groups (Goldblatt & Manning 2000: 33). Nevertheless, despite the random and sometimes wide dispersal of seeds, species with limited (in some cases very limited) distributions do occur and these are particularly responsible for the relatively high diversity in the Gariap centre (Nordenstam 1969) and in the Knersvlakte.
- (2) Overlap of distributions of species with a predominantly winter-rainfall distribution with those of species with a mainly summer-rainfall distribution, as found in *Microloma* (Bruyns & Linder 1991: 468). With respect to the timing of rainfall, it is clear from fig. 45 that stapeliads decrease in diversity with

Table 5. The number of species and endemic species for each stapeliad genus in the countries of southern Africa

Genus	Botswana Species endemic		Lesotho Species endemic		Madagascar Species endemic		Mozambique Species endemic		Namibia Species endemic		South Africa Species endemic		Swaziland Species endemic		Zimbabwe Species endemic	
<i>Australiuma</i>	—	—	—	—	—	—	1	0	1	1	1	0	1	0	1	0
<i>Baynesia</i>	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—
<i>Duvalla</i>	1	0	—	—	—	—	1	0	3	0	10	7	1	0	1	0
<i>Hoodia</i>	1	0	—	—	—	—	—	—	10	3	7	3	—	—	1	0
<i>Huernia</i>	4	0	1	0	—	—	8	1	8	0	23	16	3	0	9	1
<i>Larryleachia</i>	—	—	—	—	—	—	—	—	4	1	4	1	—	—	—	—
<i>Lavrania</i>	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—
<i>Notechidnopsis</i>	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—
<i>Ophioneila</i>	—	—	—	—	—	—	—	—	—	—	2	2	—	—	—	—
<i>Orbea</i>	11	0	—	—	—	—	6	1	8	1	24	11	4	0	9	0
<i>Pectinaria</i>	—	—	—	—	—	—	—	—	—	—	3	3	—	—	—	—
<i>Pisranthus</i>	2	0	—	—	—	—	—	—	2	0	7	4	—	—	—	—
<i>Quaqua</i>	—	—	—	—	—	—	—	—	4	0	19	15	—	—	—	—
<i>Richtersveldia</i>	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—
<i>Stapelia</i>	3	0	1	0	—	—	4	0	7	2	25	16	3	0	3	0
<i>Stapelanthus</i>	—	—	—	—	6	6	—	—	—	—	—	—	—	—	—	—
<i>Stapelopsis</i>	—	—	—	—	—	—	—	—	2	0	8	6	—	—	—	—
<i>Tavaresia</i>	1	0	—	—	—	—	—	—	1	0	1	0	—	—	1	0
<i>Tridentea</i>	1	0	—	—	—	—	—	—	4	0	8	4	—	—	—	—
<i>Tromotriche</i>	—	—	—	—	—	—	—	—	4	1	8	5	—	—	—	—
Total species [% endemic]	24	0% 0	2	0% 0	6	100% 6	20	10% 2	60	18% 11	152	63% 95	12	0% 0	25	4% 1

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an increase in the percentage of rainfall received in winter; as one approaches the west coast and the extreme south-western Cape there is a marked decrease in diversity. To some extent the presence of loose coastal sands (which stapeliads do not particularly favour) also contributes to this decrease, but rainfall, coupled with the timing of the release of seed, is probably decisive. It is mostly the case that in southern Africa the seed of stapeliads is released in November and December, during the onset of summer. Therefore, in areas where the rainfall comes mainly between April and September, this seed has low chances of germinating while fresh. Seeds of asclepiads are not viable for very long, so that seed which has had to wait out the dry summer months before germinating in April or later has considerably reduced chances of successful germination.

- (3) The juxtaposition of different rock types and soil types, each with their own endemic or nearly endemic species.

- (4) A wide range of altitude over a short distance, providing a broad spectrum of niches. Certain species prefer the higher, cooler areas and others only occur in the hotter areas at the foot of the mountains.
- (5) A wide range in depth of soils over short distances (Von Willert *et al.* 1992: 97), with skeletal soils reducing the competition from other shrubs and trees and from some of the larger and more vigorous grasses.

The area of maximum concentration of species (3320B) demonstrates all of the diversity-enhancing factors listed above except, surprisingly, the first since none of these taxa is restricted to this area. Several species with a wider distribution in the summer-rainfall areas reach this area (e.g. *Stapelia engleriana*, *S. grandiflora* and *Tridentea parvipuncta*), while several of those generally found further to the west or south, in the winter-rainfall area, manage to survive here as well (e.g. *Duvalia parviflora*, *Huernia pillansii*, *H. praestans*, *Piarranthus parvulus* and *Stapelia pillansii*). There is a remark-

ably broad spectrum of geological types here and several of the species are confined to the different rock types that are present. Thus, for example, because of the proximity here of Dwyka shales and tillites to sandstones and quartzites, *Quaqua ramosa*, *Q. pillansii* and *Q. linearis* are all found within a relatively short distance of one another, the first occurring on shales and tillites and the other two exclusively on sandstones and quartzites. This area also lies in a zone of convergence of three biomes: Nama Karoo, Fynbos and Succulent Karoo (Rutherford & Westfall 1986).

The smaller centres of diversity listed above all occur where the topography becomes more varied, so that the juxtaposition of different types of rock, a wider altitudinal range and variable soil depth, i.e. factors (3H5), are once more the main causes of this diversity. The Great Karas Mountains, Baynes Mountains and Soutpansberg-Blouberg all possess a few endemic species as well, so that the first factor also contributes in these cases. Diversification in these montane habitats is therefore signifi-

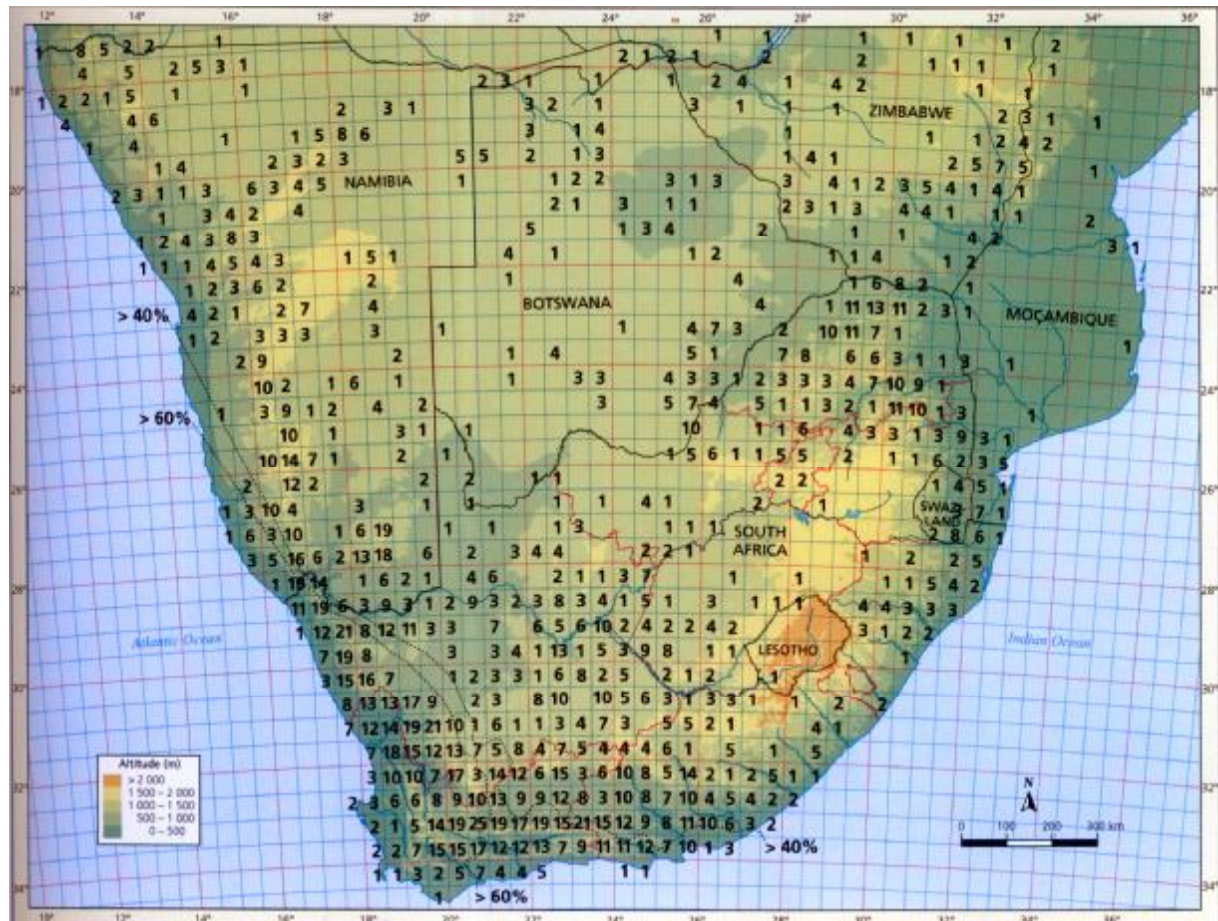


Fig. 45. Number of stapeliad species per half-degree square in southern Africa. Dotted lines: west of '> 60%' receives more than 60% of rain in winter; between the two receives 40-60% of rain in winter and east of '>40%' of rain in winter.

cant among the stapeliads, lending support to the statement of Coe & Skinner (1993) that montane isolation produces strong selection pressures.

With the relative lack of localised species or genera, the stapeliads do not fit the patterns of distribution noted by Nordenstam (1969), Werger (1978) or Hartmann (1991). Nevertheless, the centres of stapeliad diversity mostly correspond to the eight centres that were identified by Cowling & Hilton-Taylor (1994) as being especially rich in species and high in endemics. Essentially four basic patterns may be distinguished among the genera:

- (1) Predominantly winter-rainfall, within the Succulent Karoo Region and on the edges of the Cape Floristic Region, i.e. within the 'Greater Cape Flora' (Bayer 1984b; Jürgens 1991; 1997) or the Succulent Karoo and Fynbos biomes of Rutherford & Westfall (1986): *Notechidnopsis*, *Pectinaria*, *Quaqua*, *Richtersveldia* and *Tromotriche*. *Notechidnopsis* and *Richtersveldia* are endemic to Namaqualand while *Quaqua* and *Tromotriche* are especially well represented there but are not endemic. *Pectinaria* is poorly represented in Namaqualand and occurs mainly towards the boundary of the winter-rainfall region, especially on the Roggeveld.

It should be noted here that stapeliads occurring within the wetter parts of the Cape Floristic Region are never mesic elements but are found in enclaves of succulents which have developed on locally arid spots on skeletal, well-drained soils within *fynbos*.

- (2) Arid all-year-rainfall zone, on the edge of the Succulent Karoo and within the Nama Karoo biomes (Rutherford & Westfall 1986): *Duvalia*, *Ophioneella*, *Piранthus*, *Stapeliopsis* and *Tridentea*. Apart from the fairly localised *Ophioneella*, none of these genera is confined to the all-year-rainfall zone. All have representatives in the winter-rainfall area within the Succulent Karoo and even representatives occurring within the broader confines of the Cape Floristic Region. *Duvalia*, *Piранthus* and *Tridentea* have representatives in the summer-rainfall regions but there is a concentration of species along the eastern edge of the winter-rainfall region, which includes the arid parts of the southern Cape.

- (3) Namib Desert and Nama Karoo distribution (Nama Karoo Region of Jürgens 1997): *Hoodia*, *Larryleachia* and *Lavrania*. These are found along the entire length of the Namib from southern Angola to the Orange River mouth and extend eastwards along the Orange River to near Douglas and Kimberley as well as sporadically further south, in the case of *Larryleachia* to Williston and Strydenburg and in *Hoodia* to the

Southern Cape in the Little Karoo. Again there is sporadic occurrence of both genera in the neighbouring Greater Cape Flora.

- (4) General: *Huernia*, *Orbea*, *Stapelia* and *Tavaresia*. Certain species such as *Duvalia polita*, *Orbea caudata*, *O. huillensis*, *O. lugardii*, *O. lutea*, *O. maculata*, *O. valida* and *Piранthus decipiens* have a wide and very diffuse distribution over the interior of southern Africa, mainly within the Savannah biome (Rutherford & Westfall 1986) or the Sudano-Zambezi Region of Jürgens (1997). In the cases of *D. polita*, *O. caudata*, *O. huillensis* and *O. valida*, this distribution reflects to a large degree the occurrence of Kalahari sands, on which these species typically occur.

The arid to semi-arid regions of the western side of southern Africa show a diversity of succulents which is not matched anywhere else in the world (Rutherford & Westfall 1986: 61; Coe & Skinner 1993). The Succulent Karoo, with about 1600 endemic species, is the only

semi-arid region which qualifies as a 'hot spot' of diversity of global significance (Cowling & Hilton Taylor 1994). The Crassulaceae and succulent Aizoaceae are especially well represented there. The stapeliads are also an important element in parts of the Succulent Karoo. However, they have been less successful, both in terms of the overall numbers of species and in the percentage of endemic species, than the various left-succulent groups in the semi-desert areas of southern Africa that receive winter-rainfall and make up the Succulent Karoo biome. This can be clearly seen in the Cape Mora and Namaqualand columns in table 6. However, if the Nama Karoo is included then it is found that a remarkable 131 species occur, of which 72% are endemic (final column, table 6). This corresponds quite closely with the nearly 66% of southern African endemic bird species that are concentrated in the arid to semi-arid regions of the western side of the subcontinent (Clancey 1986).

It is important to note, though, that in these areas the stapeliads show nowhere near

Table 6. The number of species and endemic species per stapeliad genus in three of the floral regions of southern Africa

Genus	Cape Flora (Goldblatt & Manning 2000)		Namaqualand		Nama + Succulent Karoo + Cape Flora (A. B. C. of Jürgens 1997, fig. 1)	
	Species	endemic	Species	endemic	Species	endemic
<i>Australluma</i>	—	—	—	—	1	0
<i>Baynesia</i>	—	—	—	—	1	1
<i>Duvalia</i>	6	3	1	0	8	4
<i>Hoodia</i>	3	0	2	0	13	9
<i>Huernia</i>	2	1	3	0	11	4
<i>Larryleachia</i>	—	—	3	0	5	5
<i>Lavrania</i>	—	—	—	—	1	1
<i>Notechidnopsis</i>	—	—	1	1	1	1
<i>Ophioneella</i>	—	—	—	—	2	1
<i>Orbea</i>	4	1	1	0	13	5
<i>Pectinaria</i>	2	0	1	0	3	3
<i>Piранthus</i>	4	0	2	0	5	4
<i>Quaqua</i>	9	1	12	6	19	19
<i>Richtersveldia</i>	—	—	1	1	1	1
<i>Stapelia</i>	11	4	6	1	21	15
<i>Stapelianthus</i>	—	—	—	—	—	—
<i>Stapeliopsis</i>	3	1	4	0	8	7
<i>Tavaresia</i>	—	—	—	—	1	0
<i>Tridentea</i>	2	0	2	0	8	5
<i>Tromotriche</i>	3	2	5	1	9	9
Total species (% endemic)	49	27% 13	44	23% 10	131	72% 94

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the remarkable diversity found in *Crassula* (Jürgens 1997, fig. 9) and the succulent Aizoaceae (Jürgens 1997, fig. 6). The highest diversity of genera in the succulent Aizoaceae occurs in the Richtersveld (in the degree squares 2817 and 2917 with 50 and 53 genera/subgenera respectively, where the stapeliads have 14 and 22 species respectively). The highest diversity of *Crassula* occurs in the Worcester-Robertson Karoo on the interface between the Succulent Karoo and the Fynbos biomes. This is in the degree square 3319 where there are 61 species of *Crassula*, 15 species of stapeliad and 38 genera of the succulent Aizoaceae. Where the highest diversity of stapeliads is found (around Matjiesfontein in the degree square 3320, with 25 species), there are 53 species of *Crassula* and 44 genera of succulent Aizoaceae. Thus the number of *Crassula* and succulent Aizoaceae species always greatly exceeds the stapeliads in these areas. It is also interesting to note that neither *Crassula* nor the succulent Aizoaceae shows the same marked reduction in numbers closer to the west coast that one observes in the stapeliads. This indicates that the stapeliads have been much less successful in exploiting the benefits of winter-rainfall than either *Crassula* or the succulent Aizoaceae.

However, both *Crassula* and the succulent Aizoaceae are mainly elements of the Greater Cape Flora and their numbers drop off dramatically to the east of this region. In stapeliads the decrease to the east is not nearly so dramatic and one may deduce that they are better able to cope with the more irregular and unreliable rainfall of the arid areas east of the Succulent Karoo (Jürgens 1995).

Away from the western side of the subcontinent, the position is different, although very variable. *Crassula* is well represented along the subtropical east coast (8-22 species) and in the Drakensberg. Along the east coast stapeliads are present in low but consistent numbers of 2-8 species but they are generally absent from the Drakensberg. The latter case demonstrates the greater tolerance of *Crassula* for moisture: though skeletal soils are present, which leads to wet for stapeliads but it is tolerated by *Crassula*. Both *Crassula* and the stapeliads show peaks of diversity in the mountains of Limpopo Province along the upper mountainous reaches of the Olifants River (which forms the drier part of the Wolkberg centre of Cowling & Hilton-Taylor, 1994) and in the Soutpansberg and Blouberg in the extreme north of that province. In both these areas skeletal soils are common and the rainfall is relatively low compared to that in the Drakensberg. In fact, in the Soutpansberg 10 species of *Crassula* are found ($\pm 1/6$ of maximum), 12 species of stapeliad ($\pm 1/2$ of maximum) and ostensibly there are no succulent Aizoaceae (actually my own observations have shown that two or three genera are present



Fig. 46. The flat-topped ridges of the Great Karoo Mountains, Namibia, capped by a thick layer sandstone, are exceptionally rich in stapeliads. This view is from near the summit of Lord Hill at 2 200 m, looking south-east over some of the Schroffenstein to the Great Karas Mountains where the highest peaks reach about 1700 m.



Fig. 47. The granite massif of the Brandberg, Namibia, rises to an altitude of 2573 m out of the plains of the Namib Desert north-east of Swakomund. The upper reaches of this mountains harbour a rich and diverse flora very different from that of the plains below. Here the mountains is viewed from the north from the foot of the Märchenschlucht at about 500 m with the peak in the left rear at 1885 m.



Fig. 48. The sandstone mountains of the Soutpansberg and Blouberg, near the northern border of South Africa (white Zimbabwe) are inhabited by several stapeliads, quite a few of which are endemic. This view shows part of the Blouberg near Buffelshoek.

BIOGEOGRAPHY OF THE STAPELIADS

there, but this is still a very small fraction of the maximum number of 53). So here the stapeliads are more successful than either *Crassula* or the succulent Aizoaceae.

Jürgens (1997, fig. 8) identified the Kimberley-Douglas area as a centre of diversity for the *Titanopsis* group (of the succulent Aizoaceae) but showed that *Crassula* was poorly represented there (Jürgens 1997, fig. 9). The area from Prieska to Kimberley is also a minor centre of diversity for the stapeliads (with a maximum of 13 species found near Prieska). It appears that here the presence of calcretes and soils with a higher salt content probably excludes *Crassula* (Jürgens 1995), but the many rocky habitats with skeletal soils combined with a widespread covering of the particularly favored 'nurse-plant' *Rhigozum trichotomum* seem to be the reasons for diversity of stapeliads here. The Pofadder-Warmbad area is a centre of diversity for the succulent Aizoaceae (Hartmann 1991), *Anacampseros* (Gerbaulet 1992) and also for the stapeliads (12 species). However, in the case of the stapeliads there are no localised species within this area and the diversity, which is actually lower than that in the nearby Great Karas Mountains, is brought about by winter-rainfall taxa (*Hoodia alstonii*, *Larryleachia cactiformis*, *Quaqua*, *Tromotricha*) occurring on quartz hillsides near to other Nama Karoo taxa [*Hoodia gordonii*, *Larryleachia picta*, *Tridentea* etc].

In the stapeliads the diversity in the drier mountains of Namibia is much higher than in either *Crassula* or the succulent Aizoaceae and this brings to light various centres of diversity which have not previously been identified. The most significant is that in the Great Karas Mountains, where 18 species have been located. Another notable area is the mountains east of Rosh Pinah and Witpütz (14-16 species) and the Tiras Mountains to the north of Aus, where 14 species have been found. The Baynes Mountains, where eight species are known, form part of the Kaokoveld centre that was identified by Cowling & Hilton-Taylor (1994). A very much less prominent centre is the Brandberg-Erongo area on the eastern edge of the Namib Desert. Despite the significantly higher rainfall that the Brandberg receives in comparison to the surrounding desert (Olszewski 2000) and its remarkably diverse flora (Craven & Craven 2000), stapeliads are neither common nor well represented there. In fact, there are as many species in the Brandberg as there are in several spots (e.g. in the half-degree squares 1812 C, 2214 D) along the much more arid coast, within the 'mist-belt'. It is interesting to note as well that several species that occur in the northern Namibia extend into the arid parts of southern Angola (e.g. *Huernia urceolata*, *H. species* found exclusively in southern Angola (e.g. *Hoodia mossamedensis*, *S. parvula*) are



Fig. 49. Habitat of *Orbea longidens*, north of Manhiça, Maputo Province, Mozambique: whitish sands with short grasses, clumps of the palm *Hyphaene natalensis* and small trees of the genus *Strychnos*.

closely related to species occurring in Namibia (in the former it is to *H. pedicellata* and the latter to *S. similis*). This extension of southern Africa endemism into southern Angola is mirrored in the distribution of several bird species (Clancey 1986) and may occur in other groups of organisms.

Habitat and Ecology

The variety of habitats in which stapeliads are encountered is enormous, the one proviso always being that they must try out fairly quickly after rain. Plants are found growing in sand, on heavily loamy or stony flat areas and stony slopes, in shallow soils on solid 'whale-backs', and in a few cases on cliffs.

Sandy habitats

Sandy habitats abound in southern Africa and



Fig. 50 A slightly more arid in coastal Mozambique, typical for *Orbea halipedicola* between the Save and Zuzi Rivers, Sovala Province. Here the vegetation consists of isolated clumps of *Hyphaene natalensis* with short grasses on a finely gravelly, pale ground of more or less neutral pH.

stapeliads are found in many them. Flat sandy areas of the western Cape *sandveld* sometimes harbour stapeliads. A few species of *Quaqua* are found in this kind of habitat, especially in the drier areas further north. *Tridentea pachyrrhiza* is endemic to the arid sands around the mouth of the Orange River. The occasional specimen of *Orbea namaquensis*, *O. variegata* (in the south) or *Stapelia hirsuta* can be found in these areas as well. However, in general stapeliads tend to be rare and very scattered in them. This is in marked contrast to *Euphorbia*, where certain species are widespread in these sands, and certain genera of the succulent Aizoaceae which are also common and even endemic there (e.g. *Fenestraria* and *Woolleya*).

A considerable portion of central southern Africa is covered by what are known as Kalahari sand, which stretch from the Orange River northwards to the basin of the Congo River and Central Africa. These sand have been present for at least the past 32 000 years

(Lancaster 1989) and form the largest continuous body of sand in the world (Ballieu 1975). The more arid parts of this area are known as the Kalahari Desert, which encompasses most of eastern Namibia, most of Botswana and parts of the Northern Cape. This 'desert' is not intensely dry (receiving from 200 mm annually in the south-west to more than 500 mm in the north) but there is seldom enough water for it to seep down and avoid evaporation and there is a local lack of any perennial surface water. The sands, although often still clearly gathered into wind-formed dunes, are largely stabilized by vegetation. The extent of this vegetation and the extent to which the sands moved around by wind have fluctuated greatly with climatic changes in the region, which is thought at present to be enduring a relatively wet period (Grove 1969). Most of the solid geology of this 'desert' is obscured under a blanket of sand, but the region is mostly underlain by massive calcretes. The sands of the Kalahari are often reddish due to a fine cover of iron oxide on each grain. The region is also noteworthy for many shallow pans that have formed along the lines of sand-choked and fossilized drainage systems (Grove 1969). Although they have not been well documented in the Kalahari, stapeliads are actually fairly common in this region, where the relatively dry and rarely waterlogged conditions favour their growth. Species found in these areas mostly belong to *Orbea* (e.g. *O. caudata*, *O. knobellii*, *O. valida* etc.) but *Piaranthus*, *Tridentea* and even *Huernia* occur here.

Many of the flat, sandy parts of the tropical regions of southern Africa are (or were) covered by a dry deciduous 'forest' of such trees as *Colophospermum mopane* (*mopane*), *Baikiaea plurijuga* (Rhodesian teak), *Brachystegia* (miombo) or *Androstachys johnsonii* (Lebombo ironwood) (or *Didieria* and *Poinciana* in the sandy parts of southern Madagascar) and species of stapeliad (such as *Orbea caudata* subsp. *rhodesiaca*, *O. umbracula* or even *Australluma ubomboensis*) may grow in leaf-litter or among twigs on the floor of these fairly open forests. In Madagascar several species of *Stapelianthus* grow in sand on the floor of forests, and this habitat is especially favoured by *S. arenarius*. In tropical Africa it is mostly species of *Orbea* that are found in such habitats, often with *Duvalia polita*. The grassy, settled dunes of the KwaZulu-Natal and the southern Mozambican coast are also host to a few stapeliads, again mainly species of *Orbea*. This appears to have parallels in West Africa where *Orbea decaisneana* is common in the flat patches between grassy coastal dunes of Senegal and Mauritania (White & Sloane 1937; Plowes 1994b).

Loamy or stony flats to slopes

In the various karroid parts of South Africa and Namibia stapeliads are commonly found in



Fig. 51. The plains of the north-eastern Knervslakte, with firm red ground covered sparsely with shrublets of various succulent Aizoaceae. Stapeliads are found in these plains but a much wider selection thrives on the slopes of the mountains such as Kubiskow, which forms the backdrop here. This mountains consists of steep shale slopes quite densely covered with short bushes (especially *Pteronia incana*), with a dolerite layer forming the summit.



Fig. 52. Slopes and flats in the Asbestos Mountains north-east of Priska. This locality proved to be rich in species of stapeliad, mainly around the bases of shrubs in flat areas in the valley.



Fig. 53. Calcrete outcrops along the Aubo River south of Stampried, Namibia. The grey bushes are *Acacia nebrownii* and *Rhigozum trichotomum* (*driedoring*) and they often sheltered species of stapeliad.



Fig. 54. The very dissected country of the northern Richtersveld (the Tatasberg roughly in the centre, with white patch below summit, and the rear taken up by the Rosyntjie Mountain) viewed from a steep slope east of Rosh Pinah in Namibia. The high, dome-like summit on the left (the Stormberg) was inhabited by *Hoodia alstonii* and *Quaqua mammillaris* while *Q. incarnata*, *Stapelia similis* and *Stapeliopsis neronis* grown on the slopes from which the picture was taken.



Fig. 55. Granite domes near Ribáuè in Nampula Province, Moçambique, at about 1200 mm, covered with succulents despite the high annual rainfall of nearly 1500 mm. Here on sees a species of *Aloe*, *Euphorbia mlanjeana* and *Kalanchoe elizae*.

hard, loamy or stony ground in flats and on the slopes of hills or mountains. This is probably the type of habitat most generally associated with succulents of any kind and it is also where most stapeliads are found.

Another kind of stony habitat much favoured by certain species of stapeliad is calcrete. These are usually low, pavement-like outcrops that are generally of relatively recent origin and they are especially a feature of Namibia, Botswana and the Northern Cape (along and north of the Orange River) but they also occur further south. *Stapelia flavopurpurea*, *S. kwebensis* and *Orbea lugardii* are particularly inclined to favour this habitat. Some of these calcrete outcrops are colonised by other succulents as well, but in the Kalahari 'Desert' (eastern Namibia, western Botswana, the extreme Northern Cape), stapeliads may be the only succulents found on them. Similar formations occur in the south-western corner of Madagascar and species such as *Stapelianthus insignis* are more or less confined to them. In a more general context, calcareous outcrops are widely favoured as habitats around the Mediterranean by species such as *Caralluma europaeae* and *C. munbyana* and are also an important habitat for stapeliads in north-eastern Africa.

In the sandstone mountains of the south-western Cape, where stapeliads are rare and succulents are generally not commonplace, populations develop in locally arid spots with skeletal soils, sometime on solid outcrops. They are often found at the bases of valleys where the effects of a rain shadow are most extreme and where the temperatures are highest. In such spots there is usually a wealth of other succulents (mainly *Aloe*, *Crassula*, *Adromischus*, *Senecio* and certain succulent Aizoaceae, particularly *Oscularia*) and stapeliads are usually only found where the diversity of succulents is high.

Solid rock outcrops or 'whalebacks'

An important habitat for succulents on the wetter eastern side of the subcontinent, especially in parts of Zimbabwe and in Moçambique but also in Madagascar, is provided by the rounded domes of granite, or very occasionally dolerite as well, which form characteristic steep to gently sloping 'whalebacks'. Here vegetation develops on often very shallow accumulations of weathered grid and leaf-litter on the solid rock, forming isolated patches with a very dense mat of roots and black soil that combine to give the ground a peat-like consistency. These patches are usually dominated by the tussock-forming sedge *Coloechloa* and by various species of *Xerophyta*. Where they are not too regularly burnt, a wealth of succulents, especially belonging to the genera *Aloe*, *Euphorbia*, *Kalanchoe* and *Sarcostemma* may sometimes be found and stapeliads sometimes occur among them. In Madagascar, *Stapelianthus decaryi*



Fig. 56. A dense clump of *Huernia ericiloba* on an exposed slab of granite (same place as previous picture) at about 1200 m with *Crassula swaziensis* and a very small *Plectranthus*.

grows almost exclusively in such places, also often with species of *Aloe*, *Euphorbia* and *Kalanchoe*. The larger genera such as *Orbea* and *Huernia* have species that are confined to such habitats. They are found on 'whalebacks' widely in Mozambique (e.g. *Huernia erectiloba*, *H. hislopianii*, *H. leachii*), Zimbabwe (*H. hislopianii*, *H. occulta*) and Malawi (*Orbea caudata*) and may be more ubiquitous on such spots than is known at presents.

Cliffs

Stapeliads do not often grow on rock faces and although the occasional *Stapelia* or *Huernia* may be encountered on a ledge on a cliff face, this is not common. Outside of southern Africa it is only the rare Indian endemic *Frerea indica* which is often (though not always) found on ledges on cliffs. Within southern Africa there are only four species that are mainly cretinophilous and these are *Huernia pendula*, *Lavrancia haagnerae*, *Tromotriche baylissii* and *T. choanantha* (to a lesser extent also in *Orbea longii*). All of them grow in small pockets of soil on ledges or in cracks in the rock faces.



Fig. 57. Dolomite cliffs near Sesfontein, Namibia on which *Lavrancia haagnerae* is found.

Lavrancia haagnerae maintains the decumbent habit typical of most stapeliads. In the other three, odd stems hang down from the ledge on which they are rooted and, in *T. baylissii*, may reach remarkable lengths of up to 3 m. In *L. haagnerae* these cliffs are very exposed to the elements and especially to direct sunlight and the same is sometimes true for places where *H. pendula* grows. However, *H. pendula* and, more particularly, *T. baylissii* and *T. choanantha* mostly grow on the sides of deep, quite sheltered gorges, where relatively little direct sunlight could burn the long, unprotected stems and where high winds also do not damage them. *Tromotriche baylissii* and *T. choanantha* may be found away from cliffs growing under bushes among rocks, but *H. pendula* and *L. haagnerae* have never been observed in any other habitat. Since the seeds are wind-borne and should be able to germinate in any suitable spot (both on or off cliffs), it seems likely that predation is responsible for their not being found elsewhere.

Wherever they grow, stapeliads generally require some form of shelter or nurse-plant, at least in the early stages in their lives. Forest-dwelling species are less bothered by this requirement, growing among leaf-litter, piles of twigs or around the base of a tree. To species of more open situations, shelter is paramount, especially when the plants are young. In nature germination takes place best under bushes, around the base of a tree or between stones. In such spots moisture persists for longer than in more exposed situations and the nurse-plant also provides the young plant with protection from the sun and from being eaten. In addition, the plantlet is able to make use of the small concentrations of windblown leaf-litter and loose

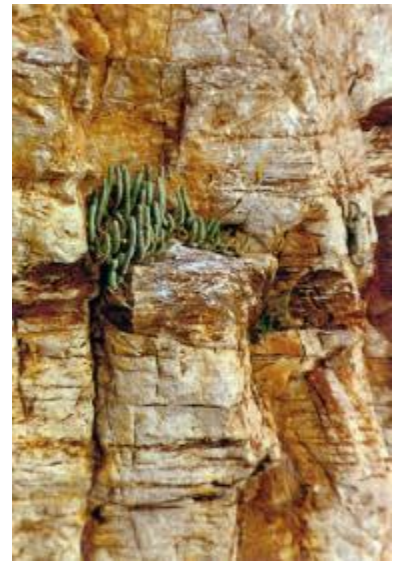


Fig. 58. *Lavrancia haagnerae* in habitat on a small ledge on a sheer dolomite cliff-face.

sand that often accumulate in such places so that the ground may be mixed with humus to a depth of several centimeters. This causes the soil to be considerably softer and more easily penetrable and also provides a ready supply of nutrients.

That these nurse-plants are vital to the survival of the stapeliad being sheltered is obvious. However, little is known about the converse effects of the stapeliad on the nurse-plant and, to my knowledge, no studies have been carried out on naturally occurring stapeliad populations. Nevertheless, the effect is unlikely to be a wholly positive one. Dunbar and Facelli (1999) reported that plants of *Orbea variegata* growing under shrubs of saltbush (a species of *Atriplex* of the Chenopodiaceae) in South Australia robbed the saltbushes of water by direct competition. Furthermore, by lowering the penetration of rainfall beneath them, they reduced the germinable seed of the saltbush and generally decreased the biomass of annual plants in the area.

In southern Africa the bushes under which stapeliads grow may be shrublets of succulent Aizoaceae (usually Ruschioideae), especially the gregarious, spiny species of *Ruschia* (*R. divaricata*, *R. spinosa* and less commonly *R. cradockensis*, fig. 59) as well as the gregarious but not spiny *R. robusta*, various species of *Pteronia* (particularly *P. pallens*, *P. paniculata* and *P. incana*) or *Rhigozum*, especially the ubiquitous and frequently dominant *R. trichotomum* (*driedoring*) and *R. obovatum* (*granaatbos*), or larger shrubs and trees of *Grewia* and *Acacia* and many other.



Fig. 59. A large specimen (about 0.3 m diam.) of *Huernia humilis* sheltering under, though beginning to outgrow, a low shrublet of *Ruschia spinosa*, PVB 5971, near Fraserburg.

The larger, shrubby species of *Hoodia* and some species of *Quaqua* tend to outgrow this shelter quite rapidly and then grow on stony slopes or flats fully exposed to the elements (Fig. 61.) In north-eastern Africa this is also common in many of the larger species of *Caralluma* and in some places (for example in eastern Ethiopia) the vegetation may even be dominated by shrubs of *C. penicillata*. The small spherical to cubiform species (in southern Africa some *Larryleachia* and in north-eastern

Africa *Pseudolithos* and *Whitesloanea*) also often grow in the open, having outgrown the bush let or stone next to which they started off. Certain species of *Huernia* (e.g. *H. loeseneriana*, *H. namaquensis*, *H. hallii* and *H. whitesloaneana*) prefer to grow in crevices in rocks and they then fill up these crevices to form very dense mats. Many plants of *Larryleachia* can also be found wedged into crevices between larger rocks, which then provide the shelter usually given by a shrublet.

Fig. 60. A small specimen of *Quaqua incarnata* subsp. *incarnata* growing among creeping plants of *Antimimna limbata* on a granite outcrop near Saldanha.



Fig. 61. A large and very exposed specimen of *Hoodia alstonii* (roughly 1 m tall) growing from a small crevice in a rock-face at the base of Koda's Peak, Richtersveld.



A very specialised ecological niche that has been successfully exploited by many succulents in southern Africa is the patches of quartz gravel that are especially common in many parts of Namaqualand and Bushmanland. Possibly as a consequence of the general lack of sheltering shrubs in such places, stapeliads are not common on them. Nevertheless *Larryleachia cactiformis*, *L. perlata*, *L. picta* (fig. 62), *Quaqua mamillaris*, *Stapelia similis*, *Tromotriche herrei* and *T. umdausensis* may be found in such places, with *l. herrei* more or less restricted to them. In these cases it seems that the seed germinates among the stones, which protect the seedlings from being devoured by animals or burnt by the sun.

Stapeliads are often difficult to find in nature. One characteristic that causes this is their tendency to grow under bushes and another is their usually extremely sporadic occurrence. Plants are often quite remarkably few and far between, to the extent that the terms 'rare' and 'population' take on a new meaning when applied to them. In such situations several hours of careful searching will reveal the presence of only 1-5 plants over sometimes a quite wide area. This is true of species of diverse as *Stapeliopsis breviloba* near Worcester, *Quaqua inversa* in Namaqualand and *Orbea valida* north of the Okavango Delta in Botswana, among many others. It is undoubtedly brought about by the very random, wind-assisted dispersal of the seeds. What is remarkable is that plants can be so scattered and yet they still reproduce successfully, as the production of seed on these scattered specimens proves.

However, not all stapeliad populations consist of such scattered individuals and most species can become locally quite 'plentiful', to the extent that in some patches there is a plant under nearly every bush. In such spots there are usually several species present, all of them in reasonable numbers. Nevertheless, they are rarely, if ever, as common as *Elytropappus rhinocerotis* (*renoster*), *Ruschia spinosa*, *Rhigozum trichotomum* or *Aloe striata* can become in a given area.

An observant traveler in the summer-rainfall areas may have noticed the remarkable tendency of species of stapeliad and *Ceropegia* to develop dense and diverse colonies in heavily overgrazed areas around villages. These colonies may consist of up to 10 species, with plants under practically every available shrublet and with many even growing in the open. This situation has been frequently observed in Botswana, Namibia, Zimbabwe, Limpopo Province and northern Cape. Concentrations of succulents, especially in the genera *Aloe*, *Caralluma* and *Euphorbia*, in disturbed areas have been documented in the Yemen on the Arabian Peninsula (Deil & Müller-Hohenstein 1985; Deil 1988). Here it was



Fig. 62. *Laryleachia picta* among quartz stones in a flattish area a little east of Wütpitz, Namibia.

found that succulent plants were dramatically favoured in some areas, the ecology of which had been modified by man. Human interference altered the competitive relationships within the vegetation (for example heavy grazing by stock could entirely eliminate certain species) and with the very long periods that these areas were inhabited, man created entirely new habitats for resettlement by plants by shifting cultivation and habitation (Deil 1988).

In southern Africa the genera *Aloe* and *Euphorbia* are not always present in such spots and a wider range of stapeliads will be found in them. The intense 'goatification' of these spots, where ever normally robust trees such as *Acacia tortilis* remain little shrubs no more than 200 mm tall, is immediately obvious (fig. 63.). It is curious that under these

circumstances the stapeliads appear not to be preyed upon, despite their often being such palatable species (even to humans) as *Orbea lugardii* or *O. maculata*. What is the cause of these concentrations?

Stapeliads are fairly slow growing (relative to other plants of a similar size in the summer-rainfall areas) and are susceptible to rot if crowded and excessively shaded. Consequently they are poor competitors against such rapid growers as grasses. These spots are notable for the paucity of grasses, which are generally the most heavily grazed elements and are therefore virtually absent from such areas. This appears to be the most important factor causing the build-up of stapeliads. Another more minor factor contributing to it might be the large amounts of animal droppings

and these have two effects. Firstly there is an increase in the available nutrients (especially the amount of nitrogen in the upper layers of the soil) and secondly there is an increase in flies, the pollinators of these plants. In addition, the greater exposure of the soil increases its surface temperature and evaporation, both of which generally cause it to have a more extreme local climate than the surroundings. A highly succulent plant such as a stapeliad is then immediately at an advantage. What is clear in these spots is that stapeliads may also exhibit a weedy, ruderal tendency when they are free to proliferate, which is very similar to that of non-succulent species such as *Gomphocarpus fruticosus*.

In the winter-rainfall areas such extreme examples are not so readily observed. Nevertheless, occasionally in Namaqualand disturbed patches dominated by *Galenia africana* also sometimes become host to remarkable concentrations of stapeliads such as *Orbea namaquensis* (fig. 64) and *Stapelia hirsuta*. Here it appears that the removal of practically all competition may allow stapeliads to flourish and this can be brought about by ploughing or even disturbance along the edge of the road. Dense stapeliad concentrations in areas which show no particular sign of degradation or disturbance are harder to explain, as are the large concentrations of *Hoodia gordonii* and the remarkable spots in the Eastern Cape where *H. pilifera* subsp. *annulata* forms the dominant shrub. The tendency for many of the seeds to lodge among the bushes near to a particular plant means that, if conditions are suitable, substantial populations can develop very locally. In some cases this is aided by just the right amount of leaf-litter being present on the ground under the shrubs, the right aspect or degree of stoniness, or a lack of other small succulents competing for the same space.

It has been observed on many occasions that, while a population of stapeliads might build up rapidly during years of good rains to the extent that a plant will be found under nearly every bush, such populations are often short-lived. Over a period of 1-5 years from first being observed, they will often disappear at that locality. There are some remarkable exceptions to this as, for example, the large plant of *Stapelia paniculata* mentioned by Leach (1985) which was at least 40 years old. This generally transient nature of stapeliad populations is in direct contrast to colonies of *Euphorbia* or succulent Aizoaceae, where plants (though not necessarily individuals) survive at a given spot for decades. This gives them a certain ability to 'move on' and colonize more suitable areas, thus escaping predators (especially insects) whose concentrations will obviously increase with the number of victims available for predation.



Fig. 63. *Piaranthus decipiens* partly sheltered by a dwarf shrub of *Acacia tortilis*, PVB 6414, Lephephe, Botswana

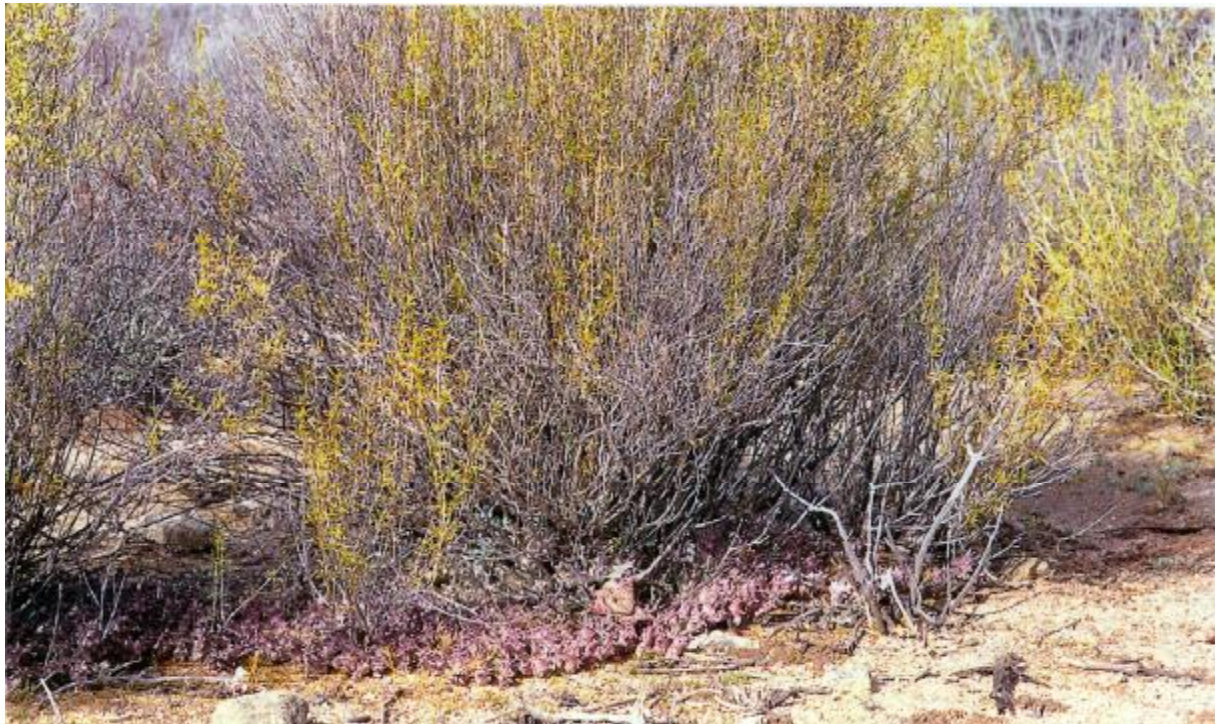


Fig. 64. A large lat of *Orbea namaquensis* (> 1 m diam.) growing around the base of a shrub of *Galenia africana* in a possibly disturbed, flat area next to a quarry east of Springbok.



Fig. 65. The region between Laingsburg and Matjiesfontein in the western Cape harbour a particularly diverse stapeliad flora, with species growing in the flats, on slopes and even on some of some of the higher peaks. The view was taken near the Rooinek Pass, south of Laingsburg.

Cultivation of the Stapeliads

Although many stapeliads grow in areas receiving mainly, winter-rainfall, most of them prefer to grow actively in spring or autumn when temperatures are higher. Hardly any growth takes place when temperatures are low, so that even if plants take up moisture and are swollen, very few new shoots are produced under these conditions. The most vigorous growing takes place when temperatures are between 20 and 30°C. Very high temperatures (> 35°C) are also not conducive to growth. This often means that in mid-summer little growth is achieved.

If it is at all possible, it is definitely advantageous to grow stapeliads out of doors. There do best in a sunny spot against a north-facing wall (in the southern hemisphere) where there is plenty of circulation of air, where they are able to experience the cool air of the night and where they may also benefit from small amounts of dew. In other words, most species generally grow better outside than in a greenhouse. However, the disadvantage of this is that they then have to be protected excessive rain. In addition, most stapeliads are very sensitive to direct sunlight. Plants that are unaccustomed to it will usually burn on exposed surfaces. In such instances the chlorophyll and surrounding tissues are destroyed, the damaged parts turn white and then blacken, becoming very prone to decay. To prevent this it is necessary to shelter the plants with a bush or some twigs. Consequently, although the results may be excellent if the right conditions are achieved, considerable effort is involved in growing these plants outside and so most growers prefer to keep them in a greenhouse.

Greenhouse cultivation of the stapeliads is best achieved in a house tables (roughly waist-height is most convenient) on which the pots can be placed, since pots on the ground are always more difficult to inspect and rapidly become neglected. Ideally, the sides between the roof and the level of the tables should be open and, at most, covered with fine-meshed chicken wire to keep rodents, cats and birds out. These open sides allow as much free movement of air as possible. In colder climates where such an 'open' house is impractical, circulation of air can often be achieved with a few small electric fans such as those that are used to keep the processor in some computers cool. A few growers favour having tables that hold a shallow layer of soil (5-8 cm deep) and form beds. Heating cables can be placed in these beds if necessary. Either pots can be embedded in the beds, or the plants can be grown directly in them. The latter situation may favour and even assist the rampant growth of some vigorous stapeliads, but it rapidly becomes difficult to control diseases and to keep different plants separate, with the result that information may be lost. Most growers therefore prefer to keep their plants in separate pots.

Propagation Growing media

There is no 'best' soil mixture or growing medium for the successful cultivation of stapeliads. In fact, they will grow under suitable conditions in practically any soil, provided it is not too alkaline. Therefore the development of a suitable mixture in which to grow them is largely a matter of combining personal taste with experience and with what is available.

It is possible to grow them very successfully in a hydroponic mixture consisting of peat, perlite and vermiculite mixed in the ratio of approximately 2:1:3 or 4. This somewhat acidic mixture is very light and easily penetrated by roots, is reasonably well aerated and in many ways resembles the concentrations of loose, partly decomposed leaf-litter under trees and bushes in which stapeliads often grow naturally. It is best to water this medium by soaking the pots, since water poured on often runs through rapidly but leaves dry patches in the pot. Once properly watered by drenching, the mixture remains moist beneath the surface for up to a month (depending, obviously, on the depth of the pot). Therefore watering should be organized so that the contents of the pot do not become dry too long, nor remain constantly wet below the surface. Since this medium is sterile and pretty well devoid of nutrients, plants in it need to be fed regularly (that is, at least once a month during spring) with some soluble fertiliser. This mixture has to be replaced after 1-2 years since, with time it tends to become denser and poorly aerated and plants in it begin to stagnate.

Some growers cultivate stapeliads very successfully in pure river sand, a mixture that is also virtually sterile. As it has no organic

component, it is necessary to feed with soluble fertiliser from time to time. Even better results are often achieved with a mixture of cleaned river sand (or filter-grit) and compost in the ratio 2:1. I personally prefer there to be some soil component to this (one part soil and one part compost to three parts river-grit). There are other very successful growers who keep their plants in a coarse, gravelly granitic soil such as may be found in many parts of Namaqualand. A fine-grained, acidic black soil that occurs in parts of Cape Town has been found to be excellent for growing stapeliads, especially plants that originate in regions where the soils derive from sandstones (and are generally acidic), but also for other species. Such soils have a high but very well decomposed organic component which stapeliads appreciate. It is also probable that the plants' habit of growing in small accumulations of leaf-litter, which are also somewhat acidic, may cause them to find this type of soil very conducive to vigorous growth.

It is important, though, if a newly produced compost is being used, to make sure that it has been sterilized. Heating it to between 60 and 80°C or slightly more kills off any fungi or bacteria which could later cause trouble, as well as weeds whose seeds are dormant in the compost.

Whatever mixture is used, it is essential to temper the amount of water given and its frequency of application to how rapidly the soil mixture dries out after a substantial watering. This is most important since the roots of stapeliads are particularly prone to rotting if they remain moist for prolonged periods, especially in the warmer months when fungal activity is rapid and frequent. Very shallow pots will dry out within a day, if kept in a warm spot with



Fig.66. A magnificent crested specimen of *Hoodia flava* about 25 cm in diameter, in habitat near Fraserburg. This malformation may also be related to that known as witches broom.

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vigorous circulation of air, and they must be watered once or twice a week if one wants the plants to grow. Deeper pots should be watered at least once every two weeks during the growing season. Stapeliads seem to appreciate being indulged with liquid or soluble fertiliser and this assists in stimulating new growth. An application of such a fertiliser with the water once a month or so, especially during spring, leads to much-enhanced growth.

Particular care should be taken when growing stapeliads that root by a single, central stem only. This includes all species of *Hoodia*, all *Laryleachia* species, some species of *Quaqua*, and many species of *Pseudolithos* and *Whitesloanea*. It seems that in most stapeliads roots constantly and naturally die off and are replaced by new roots. Under the restrictive circumstances of a pot, stem can easily rot off as well. In the species with a single central root system, the risk of the central axis rotting off is much higher and consequently more care should be taken to prevent decay. This is most easily arranged by keeping the plants in a more gravelly soil with lower (or even no) humus content. It also helps to grow them either in clay pots, where the contents dry out more quickly than in plastic pots, or in smaller plastic pots. In addition, one should water them far more sparingly, allowing longer periods between watering.

Repotting

A cactus or *Euphorbia* planted in a large enough pot can be left for years, even decades, without adverse effect. Indeed, such plants flourish for long periods in the same soil and pot, preferring not to be disturbed. In general this is not true of stapeliads.

Stapeliads tend to be fast growers if given the right stimuli (these include a reasonably high humus content of the soil, an increase in temperature and some water) and, when growing vigorously, they produce an enormous number of roots. After a year or sometimes only six months of vigorous growth a dense mass of roots develops and this fills up the pot (fig. 67). New roots then arise less frequently, older roots



Fig. 67. A thoroughly root-bound specimen of *Huernia* after removal from the pot in which it had been growing of two years.

atrophy and often decay and the plant will lapse into prolonged inactivity. It often gradually assumes an unhealthy yellow to pale reddish colour that is quite different from the colour of new growth and this can be the prelude to parts of it dying off as fungal invasions from the roots spread into some of the stems. This might seem to be the very opposite of natural, but in habitat too the older stems constantly atrophy as the plants age. In the field it will often be observed that mat-forming plants tend to spread out away from their point of origin and the older stems gradually die off and vanish. It is important to realise that many of these habitats experience irregular and unreliable rainfall and generally much harsher conditions than exist in the greenhouse. Consequently, by watering regularly we often cause cultivated plants to grow much faster than they would in their natural habitat and so this process of attrition will happen sooner and more rapidly in a potted plant in the greenhouse than it does in habitat.

Inattention to and a lack of understanding of this phenomenon, in addition to problems with certain diseases, has led to the notion that stapeliads are 'difficult' and ephemeral in cultivation. Often one becomes aware of problems only too late, when fungal infections have spread from the roots into the vascular systems of many of the stems and more or less nothing can be done to save them.

The only palliative for overcrowding of the roots is periodic repotting and usually this should happen at least once every two years. When this is done, the plants should be removed carefully, any old and dying or discoloured stems must be cut away and discarded, and the roots trimmed back to a length of 10-20 mm. Any dead roots should be cut back right against the stem. This rather ruthless treatment may seem heartless, but the plants' ability to generate new roots under favorable conditions is generally underestimated. It is also important to know that clusters of disturbed and possibly slightly bruised roots are much more likely to rot and take parts of the plant with them. Do not plant the trimmed plants back immediately. They are best left for 2-4 weeks (or longer) so that any damaged tissue can dry out and form a callus. To assist this process and prevent any fungal infections, cut stem and even the roots can be dusted with powdered sulphur. Repotting can be done at any time of the year it is most successful during late winter, so that by early spring the plants are back in pots and can receive some water later in spring to help them back into growth.

It follows that a stapeliad collection is far more labor-intensive than a collection of other succulents would be. However, if this process of regular repotting is rigorously carried out, the effects of overcrowding of the roots are avoided. In addition, it is possible to control

diseases that may be lurking below the soil (see later) and individual plants can remain in cultivation for years.

Propagation by cuttings

Most succulent asclepiads are readily propagated by cuttings. There are a few species of stapeliad that cannot be grown from cuttings. In these species cuttings, however large, rarely root and somehow the stem seem to have lost the ability to produce adventitious roots. *Quaqua mammillaris* is one of these and the same seems to be true of *Hoodia gordonii*, *H. alstonii* and *H. triebneri*. *Quaqua ramosa* and *Q. pillansii* are also reluctant to root from cuttings, but will in fact do so on occasion. The remaining species of *Hoodia* and *Quaqua* grow easily from cuttings, so this recalcitrance of a few species is not a generic trait.

Many, if not most, stapeliads have the ability to produce roots anywhere along the stem if the right stimulus is given. In particular, stems that have rotted away towards the base often manage to set up a barrier beyond which the rot does not spread. However high up the stem this barrier is, the remaining piece will usually root and, with time, may establish a new plant. Similarly, cuttings will in fact root wherever they are taken provided that, when the cutting is made, the piece taken does not simply shrivel up i.e. it must not be too small. However, if one has any choice in the matter, cuttings are best taken where a younger stem joins an older one and, to prevent drying up, the younger stem should not be too small. The prospective cutting should be cut off with a sharp, clean blade and both surfaces dusted with sulphur to assist in callus formation. The cutting is best left for 2-4 weeks for the callus to form properly and then it may be planted. When it is planted, it is often best to prop up the cutting with one or more stones around its base. This stabilises the plant in the soil so that movement which might damage any newly formed roots does not occur. It also prevents developing roots from pushing the cutting out of soil and, in addition, it may induce a slightly moister micro-climate under the stone which is more conducive to rooting. Rooting can be very rapid, especially if the cuttings are taken in spring, but can also take several months and patience may be necessary. A bed with under-soil heating will definitely expedite matters. Rooting is rapidly accompanied by swelling of the stems and by growth, so it is usually quite obvious when the cutting is beginning to establish itself.

Propagation by grafting

Certain species of *Caralluma* and *Quaqua*, most species of *Pseudolithos* and *Whitesloanea crassa* rot so readily if grown on their own roots that, to ensure their survival in cultivation, they can be grafted onto plants with a more resilient root system. Once this has been done, the

plants may be watered regularly and growth is often strong and rapid. Certainly the risks of a valuable plant being lost are much reduced.

As the base (or 'stock') onto which the difficult plant is to be grafted, a vigorous and resilient clone of a *Stapelia* (*S. gigantea*, *S. hirsuta* or *S. leandertiae*) or an *Orbea* (*O. variegata* or *O. verrucosa*) can be used. The stock should be established and growing vigorously before it is used, since a week stock will not fuse strongly with the piece to be grafted and might itself shrivel up on being cut. When it is decided to graft, cut the stock cleanly and horizontally about 20 mm above the soil, using a very sharp, clean and sterilised blade. Trim back the angles on it slightly so that they do not shrink upwards as the surfaces dry out and interfere with the piece that is grafted onto it (the 'scion'). Cut the scion similarly, again trimming back slightly any angles, and make sure that there are no pieces of epidermis protruding. On the stock and scion the vascular traces will be seen clearly as darker spot in a green matrix. When placing the scion on the stock, try to make sure that there is some zone of intersection between the two sets of vascular traces. The scion should not, as far as is possible, project out over the edge of the stock, so it is better for it not to be thicker than the stock. It should sit firmly and sturdily on the stock, and it is often useful - but not essential - to hold it gently in place with a small wire support pressing on its apex. It can be difficult to stabilize a long scion until it has fused to the stock and consequently smaller straight pieces (20-50 mm long) are by far the easiest to work with. Once the graft has been completed it will usually take up to a week for the necessary joining of tissue to take place. After this, one may already begin to see signs of some swelling in the scion as it takes up water and nutrients from its adopted root system, and soon the terminal bud begins to develop. Any support may then be removed.

Using a stapeliad as the stock has its attendant risks. In particular, it too may be prone to rotting if overwatered. As a consequence, many people who propagate stapeliads prefer to use the tubers of the now more or less cosmopolitan ornamental *Ceropegia linearis* subsp. *woodii*. This plant is extremely tough, to the extent of being almost indestructible, and the use of it greatly reduces the risk of rotting. I have also found some forms of *C. africana* subsp. *barklyi* to be similarly tough. *Ceropegia linearis* subsp. *tenuis* is also very resilient, but it tends to lack the vigor of subsp. *woodii* and is not recommended.

Again one must ensure that the tuber to be used as a stock is established and growing, with some of its surface projecting from the soil. Here one should make certain that the diameter of the scion is rather smaller than that of the tuber onto which it is to be grafted. Slice

horizontally a layer 1-2 mm thick off the top of the tuber. It will be noticed that the vascular systems forms a ring a short distance beneath the epidermis and it is necessary to make sure once more that this ring and the vascular traces of the scion intersect. It is easier to ensure that the vascular traces intersect if the scion projects slightly over the edge of the stock. However, such pieces can be more difficult to hold in place, and shrinkage of the edges of the cuts may cause problems. It is useful in this situation to hold the scion on the stock lightly to ensure that contacts is made over as wide an area as possible. If plenty of sap is present when the cuts are made, this will, on drying, often act as an excellent binding agent for holding the two pieces together until they have fused and thus it is not necessary to hold the scion on physically.

Propagation by seeds

Seeds of stapeliads are generally difficult to obtain in any variety or quantity. However, now that the method of pollination is more widely understood, some growers are able to pollinate their plants and so this situation has improved. If seeds are obtained, they are an extremely easy method of propagation. Seeds can be planted fairly soon after they have left the pod (within two weeks) but should not be kept too long: they seem to lose their viability after about one year and seeds that are over two years old generally do not germinate. It appears that if they are stored in a deep-freeze, their period of viability can be extended indefinitely, but it is then essential to ensure that the seeds are quite dry before they are frozen.

Various mixtures can be used to germinate seed but I have found the hydroponic peat/perlite/vermiculite mixture described above to be the most effective. This is especially since it retains moisture for long periods without being waterlogged (assisting the young seedlings in their first weeks) and it is loose and well aerated and thus may be fairly similar in texture to the accumulations of left-litter under bushes in which stapeliad seeds mainly germinate. Having nearly filled the pot with this mixture, flatten it down lightly and then insert the seeds into it with the micropylar end nearly vertically downwards. It is advisable to insert each seed with a pair of tweezers, making certain not to break the seed in the process (pieces of the margins may break off but this is not significant), pushing it in so that the whole seed just disappears beneath the surface. This is a somewhat tedious procedure but it maces certain that each seed is inserted the right way up and that they are neither too crowded nor too close to the surface where they might dry out. Now soak the whole pot overnight in water mixed with fungicide, to make sure the mixture is wet right through. Remove it from the water and keep it in a shady but warm place in the

greenhouse. There is no need to cover the pot with glass or paper to prevent the surface from drying out, but it might be necessary to repeat the watering after a week or two, or to water lightly from above every 2-3 days to prevent the upper layers from becoming too dry.

Many stapeliad seedlings already begin to emerge 1-3 days after the seed has been planted (this is in fact not the quickest known in the asclepiads, since *Fockea* seeds may germinate within 18 hours). Some take longer than this and a few may take up to two weeks. The seedlings grow rapidly to put out their cotyledons and their first pair of leaves but they are very susceptible to fungal attacks in their early stages and this is why the pot is soaked in the beginning in water containing a fungicide. It is usually not necessary to repeat this anti-fungal treatment. Once two or three pairs of leaves are out it is time to consider repotting the plants into a normal soil mixture, though they can remain in the hydroponic mixture for up to a year. Seedlings of difficult species can be grafted in these early stages if it is thought necessary (cut them off 4-8 mm below the cotyledons). Such seedlings are, of course, very slender and when they are cut it will be found that their vascular tissue forms a very small ring indeed. These plantlets can be grafted onto a tuber of much larger diameter by simply placing the centre of the cut seedling over the vascular ring of the tuber, thereby ensuring that their vascular traces intersect. It is advisable to place the seedling well within the edge of the epidermis of the tuber since this will shrink with time and may interfere with the process of joining the tissues.

Diseases

Stapeliads are prone to several diseases which can kill whole plants very quickly. It is most distressing to find a special plant, which seemed healthy, collapsed in a translucent, jelly-like heap from which it cannot be saved and for which there is no apparent reason in the first place. However, these diseases often give signs of their development in a plant before they reach a dangerous level. It is therefore important to keep the collection under constant surveillance. In particular, it is necessary to watch for any changes of colour in the stems or unexpected discoloration of tiny, recently produced leaf-rudiments if these are present. These changes often herald imminent disaster and, if action is taken quickly, much can be saved.

Fungal attacks on stapeliads take many forms, some more pernicious than others. Black rot is a particularly disfiguring fungal disease which causes black spots of various sizes to spread on the surface of the stems. However, it spreads only slowly and can be checked by painting on concentrated fungicide. If left

Cultivation of the Stapeliads

untreated, the stems eventually shrivel up and the whole plant can die.

Downy mildew attacks new growth, causing it to become covered with a fine, whitish fur of spore-bearing threads which eventually cause it to shrivel up. Treatment by painting on concentrated fungicide checks spreading but it is not clear whether this treatment kills the fungus or merely temporarily inhibits it. Treatment with the systemic fungicide 'Apron C' (active ingredient metalaxyl) is reputed to be effective and is also very effective for the treatment of damping-off in seedlings.

Perhaps the most dramatic fungal attacks are those in which the whole plant turns into a translucent, jelly-like mass. This is a consequence of attack by *Fusarium* and it is not known whether this can be controlled with a fungicide. Generally if this is noted before it is too late, it is best to remove the whole plant, clean off any infected areas, get rid of the soil (or re-sterilise it) and start the plant off again after letting it dry out for some time. During this drying time other stems will often dry up and atrophy as well, but usually the fungal attack runs out of steam and some parts of the plant survive.

The most pernicious insect pest on stapeliads is the so-called mealy-bug. This is a small, slow-moving, soft and pink insect which covers itself with a waxy secretion somewhat resembling white flour. Several species appear to be involved (Malumphy 1996). This pest first appears above ground, usually in the grooves of the stems towards their apex, and it appears that some of them gradually begin to migrate beneath the soil where they attach themselves to the roots and around the joins of the roots to the stems underground. The insects suck liquids from the plants, weakening them as they do so. Although their feeding is debilitating to

the plant, this is usually not the main cause of trouble. In their sucking activity, they injure the surface of the roots and underground stems, making them extremely vulnerable to fungal attack. Thus it is very important, whenever a concentration of stapeliads is kept together in pots, to ensure that they are free of mealy-bug. To ensure this, many growers spray regularly (once a month) with an organophosphate such as Chlorpyrifos. However, if by oversight the mealy-bugs become too entrenched and move to the roots, drenching with a systemic organophosphate containing the active ingredient 'dimethoate' is the best method of ridding the collection of them. The dangers associated with using this substance are well known, but fortunately more environmentally friendly 'green' systemic are now available, such as those containing the active ingredient Imidacloprid, a derivative of nicotine, which is sold under names such as Cofidor (Barad 1996), Marathon or Admire.

The red spider mite (otherwise known as two-spotted spider mite, of the genus *Tetranychus*) is another pest to which stapeliads (especially members of certain genera such as *Hoodia* and *Thodonta*) are susceptible, though the mite is even more of a nuisance on the more leafy asclepiads. These minute vegetarian mites are so small that they are not easily seen. They cause discoloration of the surface of the stem and leaves where they penetrate them to suck out the sap (the discoloration is caused by the death of cells where the mites' mouthparts penetrate) and they also spin a fine protective web over the surface of the plant. Red spider mites thrive in dry, still, warm conditions and under conditions of water- and nutrient-stress. Increasing the circulation of air around the plants helps to avoid some of these problems. Daily misting with water has been

suggested, since the mites dislike moist condition. However, this seems to cause some of the more sensitive stapeliads to rot, so it is not likely to be a good solution. There are two cures for this pest. One involves biological control, which can be achieved with the introduction of a predatory red mite (of the genus *Phytoseiulus*) which lives off the red spider mite. This, however, is not universally available and it is also very sensitive to the use of any poisons on the collection. The other cure is treatment with poison, either an acaricide (such as Kelthane or Omite) or another broader-spectrum poison such as Chlorpyrifos. Since new generations of mites appear within a few days, it is necessary to repeat the procedure several times within 1-3 weeks to prevent the collection from becoming infested again. Red spider mites rapidly develop resistance to sprays, because of their very short generations, and then they are difficult to control. They also spread on the wind from surrounding vegetation, with the result that infestations often will reappear quite quickly, despite apparent eradication.

The rather unsightly affliction collectively known as witches' broom is occasionally found in stapeliads. Here the terminal bud of a stem becomes disorganised and produces irregular and misshapen tubercles that are often partly fused and often have a rough surface. This condition is regularly seen in the field (especially in *Hoodia gordonii*, fig. 68) and causes the plant to be unsightly and produce disfigured flowers or no flowers at all. Witches broom is found in many plants, both in cultivation and in the wild, and it is caused by different agents in different plants. In the Amazon cacao plant it is caused by a fungus (Dias *et al.* 2000); in some other cases it has been established that witches' broom is caused by phytoplasmas, which are very small bacteria without cell walls (Lee *et al.* 1998). Such detection has only been possible using recently developed molecular-based techniques similar to those used in the study of DNA-sequences for systematics. It has also been established that these phytoplasmas are transmitted by mites or thrips when they are feeding on or probing for suitable feeding-plants (Oldfield & Proeseler 1996). In South Africa it has been established that witches' broom in *Protea* is caused by phytoplasmas transmitted by Eriophyoid mites (R. Newton, pers. comm. 2002). Little is known about this phenomenon in succulents. Eriophyoid mites (apparently belonging to the genus *Aculus*) have been detected on plants of *Hoodia gordonii* suffering from witches' broom and it is suspected that the disfigurements are caused by a reaction of the plant to the saliva of the mites (S. Naser, pers. comm. 2003). Treatment for this disfigurement does not exist apart from cutting off (and destroying) the affected parts. The plant will often recover in due course and produce normal growth again.



Fig. 68. A specimen of *Hoodia gordonii* suffering from witches broom, east of Witpütz, Namibia.



Fig. 69. A larva of *Paramecops stapeliae* removed from a stem of *Stapelia engleriana*.

There are several other pests that can do considerable damage if not spotted early enough. The *Stapelia* weevil *Paramecops stapeliae* (fig. 69) belongs to a widely distributed but small genus of snout-beetles which generally feed on the fruits of asclepiads of many kinds (Oberprieler 1988). *Paramecops stapeliae* is recorded widely over southern Africa from the Little Karoo to Zimbabwe and Namibia but appears to be endemic to this region. It is only known to feed on stapeliads and it is also the only species that lives on the stems. The adult weevil, which is a little over 10 mm long, eats distinctively shaped cavities out of the stems and deposits eggs in small holes which it makes near the base of the stem. Once the larva (a white grub, in the final stage up to 20 mm long) hatches, it tunnels through the stem and hollows it out. This destroys the stem completely and can lead to the death of large parts or the whole of the plant. *Paramecops stapeliae* has been recorded on many different stapeliads, including several species of *Huernia*, *Quaqua* and *Stapelia* (Tribe 1984; Oberprieler 1988; Meve 1995b). It has also been observed on species such as *Stapeliopsis saxatilis*, *Tridentea gemmiflora*, *Tromotriche herrei* and *T. pedunculata*, and even on small-stemmed species such as *Piarranthus* and *Pectinaria*. It is generally not common, except sometimes in spots where a build-up of species has occurred, but it is especially prevalent in years of good rainfall when it can decimate such populations.



Fig. 70. The larva of the Butterfly *Danaus chryssipus*, here feeding on stems of *Orbea variegata* on Lion's Head, Cape Town. These can be quite a nuisance in collections in Cape Town (photos: G.D. Tribe)



Fig. 71. The aphid *Aphis nerii* parasitizing a plant of *Caralluma turneri* in cultivation in Cape Town.

It can become a destructive pest in collections if these are kept where stapeliads occur naturally, but can be controlled with broad-spectrum insecticides.

The attractive and striking larvae of the African monarch butterfly *Danaus chryssipus* (fig. 70) are often seen on asclepiads and can eat the young and tender parts of stem of plants that are grown outdoors. They are easily seen and can be removed by hand.

A quite colourful species of aphid, the oleander aphid *Aphis nerii*, which has a yellow body and black appendages, is commonly predatory on species of *Apocynaceae* such as *Nerium*, *Vinca* and many asclepiads as well (*Asclepias*, *Cynanchum*, *Gomphocarpus*, *Hoya* etc.). This tropical to warm-temperate pest has been observed on several species of *Ceropegia* and on slender inflorescences of *Caralluma turneri* (fig. 71) in cultivation. It tends to form large colonies, 'flush-feeding' on new growth on free nitrogen that is being moved to the growing tips of the stems by the plant. The aphids tend to excrete excess carbohydrates as a sugary fluid on which an unsightly black mould may grow. Their activities also lead to the stunting of new growth (Millar, pers. comm. 2002).

The fruits of many stapeliads (and other asclepiads) are frequently parasitised by small fruit-flies of the genus *Dacus* of the Tephritidae (fig. 72). Here it appears that the adult fly deposits eggs near the tip of the follicle, the larvae eat their way through the seeds and pupate towards the base of the pod (G.D. Tribe, pers. comm. 2002). In spots where plants such as *Hoodia gordonii* are common and produce large numbers of pods, this parasite is very destructive and most of the pods will be found to be devoid of viable seeds. However, it has been found that the larvae of these flies are themselves parasitised by a small wasp (Meve 1995b), so they can be biologically controlled in nature. Larvae of these flies are occasionally

found inside stapeliad fruits in cultivation.

Scale-insects are not often a problem with stapeliads except for a relatively large (2-3 mm in diameter) yellowish scale which was one time a considerable pest at the Karoo Botanic Garden in Worcester. Although not destructive, it is debilitating to the plants and causes considerable malformation of growth. These animals proved very resistant to most treatments. It was found that brushing with concentrated Malathion and the physical removal of each scale-insect were the most effective.



Fig. 72. *Platycorynus dejeani*, found feeding originally on stems of *Stapelia schinzii*, Opuwa, Namibia (photos: G.D. Tribe)



Fig. 73. The fruit-fly *Dacus bistrigatus*, which parasitizes enormous quantities of seed on stapeliads, here after emerging from a pod of *Fockea edulis* collected near Robertson in the West Cape (photos: G.D. Tribe)

Uses of the Stapeliads

Many members of the Aposynaceae in the strict sense are extremely poisonous. Thus, for example, various poisons are known in members of such genera as *Acokanthera*, *Adenium*, *Nerium*, *Pachypodium* and *Strophantus*. Some of these poisons are extremely dangerous and several of these plants are even famous as providing poisons for arrows (Watt & Breyer-Brandwijk 1962). In addition (and despite their toxic content) several species of *Nerium*, *Plumena*, *Strophantus* and other genera are widely grown and are well known as ornamentals. Members of the Asclepiadoideae have a far less vicious reputation. Whereas a few species of *Cynanchum* and *Gomphocarpus* appear to be poisonous, *Calotropis procera* has many uses, including the treatment of impotency (Watt & Breyer-Brandwijk 1962). Although the tubers of many members of the Ceropegieae, such as *Brachystelma* and *Ceropegia*, are eaten in rural areas, the stapeliads themselves are not widely put to use. They have always had a presence in specialist collections but they were, until recently, rarely cultivated for any other purpose. One exception to this is *Caralluma adscendens* var. *fimbriata*, which is cultivated in Myanmar in the central dry zone (fig. 74) and is quite widely available as a vegetable in the markets. It is reputed to be helpful in curbing heart ailments.

In southern Africa, the young foliodes of most species are eaten and in many cases the flowers are also eaten. When they are turgid after rains, the stems of certain species are also consumed and many of them have a pleasant, if somewhat bland, lettuce-like flavour. Examples of these are *Bainesia lophophora*, *Australluma*

peschii and the species of *Ophionella*, *Pectinaria* and *Thdentea*. Certain species of *Orbea* such as *O. lugardii* and *O. maculata* are also consumed and also have a lettuce-like flavour. Many on these edible species are known locally as *gortjie* or *agurtjie*, or more rarely as *ghaap* in the case of *Pectinaria*. Other species of *Orbea* such as *O. namaquensis* are eaten as well but have a slightly bitter taste (the flowers of this species are also eaten and are locally known as *poesblom* on account of their lurid colouring). Yet other *Orbea* species are carefully avoided, being unpleasant to the taste. Similarly, *Stape-liopsis exasperata* is edible whereas the other species of *Stape-liopsis*.

All *Hoodia* species are edible. *Hoodia officinalis* was originally imported to the USA as a treatment for piles (Brown 1907-09: 894) and the use of *H. pilifera* against hemorrhoids in southern Africa is recorded as well in Watt & Breyer-Brandwijk (1962). The more widespread species such as *H. flava*, *H. officinalis* and *H. pilifera* are commonly known as *ghaap* and are widely prized by rural dwellers for their edible stems. Stems are broken or cut off and then rubbed on a stone to remove the spines, after which they are cut into strips and eaten. They have a peculiar, pervasively spreading, sweet taste which is remarkably persistent and is said to quench thirst and hunger for extended periods. Some farmers have mentioned that at one time a tasty preserve was made from the stems but this practice seems to have stopped.

The large, hard-spined species such as *H. alstonii*, *H. currorii* and *H. gordonii* are more rarely eaten but there are nevertheless people who seem to consume them with relish. Their lower status as food is indicated by names like

muishondghaap or *jakkalsghaap* or *ghobba*. They have a more bitter flavour that spreads around the mouth and is difficult to get rid of.

At the other end of the spectrum are the species that are never eaten. This includes all species of *Duvalia*, *Larryleachia*, *Piarranthus*, *Stapelia* and *Tromotricha*. Many of these have a strong, bitter flavour and are known as *kopseer*, since their bitterness is said (probably erroneously) to induce a headache. The species of *Larryleachia* in South Africa are well known to be very unpleasant and have an extremely strong, bitter taste. They are widely, but almost certainly falsely, considered to be poisonous. Nevertheless, they are mostly well known where they occur and their phallic shape has led to all manner for them, such as *hondebal* and *perdepiel*, or even (getting away from the phallic) *meidepram*. More respectable names for them are *bobbejaan-seep* or *honde-seep*, alluding to their somewhat slimy sap.

The reputation that some species of *Hoodia* have for quenching thirst and hunger has led to an investigation by the Council for Scientific and Industrial Research of South Africa and various international pharmaceutical firms into the commercial production of the relevant active principle and the registration of a patent for it (reported in *Time*, August 6, 2001, in which the plants were referred to as 'the *Hoodia* cactus!'). Certain *Hoodia* species are being grown from seed for the extraction of this substance as a cure for obesity. It has been found that the active principle is produced in greater amounts when the plants are grown in more or less natural conditions. This has led, for the first time, to the cultivation of *Hoodia gordonii* on a significant scale near Upington along the Orange River, where they occur naturally and to the monitored, commercial exploitation of some large populations.

On a quite different note, *Orbea variegata* is regarded as a dangerous pest in South Australia. It was first observed there in the semi-arid area near Port Augusta and Whyalla in 1967. Initially it was only detected on stony hillsides but it was later found to be thriving in low-lying areas of saltbush (*Atriplex*) shrubland with deep soils, where it had a deleterious effect on the shrubland. The wind-dispersed seeds had enabled it to move some distance from where it was first recorded (Dunbar & Facelli 1999).



Fig. 74. Cultivation of *Caralluma adscendens* var. *fimbriata* at the village of Kabani near Nyaung U in Myanmar. Plants are propagated by taking cuttings and are cultivated in slightly raised beds under leaves of the toddy-palm *Borassus flabillifer* which are held above them on the wooden frame visible here. These plants are sold on the market.

Systematic account

Key to the Genera in Southern Africa and Madagascar

1. Outer and inner series of corona lobes vertically well separated on staminal tube and neither partly nor wholly fused to one another (outer corona often disc-like) 2.
2. Leaf-rudiments with small stipular denticles, corona raised above base of tube on stipe, outer series resting on rim or sides of small cupular tube formed entirely by annulus **Duvalia**
2. Leaf-rudiments without stipular denticles, corona very rarely raised above base of tube on stipe (c.f. *H. kennedyana*), outer series spreading on base of tube and often partly fused to it, tube often with annular thickening around mouth but not formed entirely by annulus **Huernia**
1. Outer and inner series of corona lobes not vertically separated on staminal tube and partly or wholly fused to one another 3.
3. Tubercles on stem arranged into 6 or more angles 4.
4. Inflorescence usually only 1 per stem near base 5.
5. Leaf-rudiment slightly sunken into apex of obtuse tubercle and < 1 mm long **Lavrania**
5. Tubercle tapering into leaf-rudiment which is not at all sunken into apex of tubercle, leaf-rudiment at least 2 mm long 6.
6. Tubercles each tipped with 3 sharp spines, outer corona with long slender lobules each tipped with tear-shaped knob **Tavaresia**
6. Tubercles each tipped with single soft bristle or minute leaf-rudiment but not with spine, outer corona bifid into narrowly deltoid lobules without apical knobs **Stapelianthus**
4. Inflorescences several per stem, mainly towards apex 7.
7. Each tubercle on stem armed at apex (at least when young) with a spine (1.5–3–15 mm long) **Hoodia**
7. Each tubercle on stem with small persistent and not spine-like leaf-rudiment < 1 mm long or leaf-rudiment absent 8.
8. Stems with 10 or more angles, each tubercle with small conical leaf-rudiment usually sunken into apex **Larryleachia**
8. Stems with 6–8 angles, leaf-rudiment not distinguishable from tubercle 9.
9. Inflorescences each with single flower and single not flattened bract, outer corona forming pectinate ring around gynostegium, pollinia broader than long **Pectinaria**
9. Inflorescences each with several flowers and bracts (basal bract distinctly flattened), outer corona not pectinate, pollinia longer than broad 10.
10. Stems rhizomatous with erect apices, 20–25 mm thick, tubercles tapering to acute tooth, corolla (10–)12–17 mm diam. **Richtersveldia**
10. Stems procumbent with prostrate apices, 9–15 mm thick, tubercles flat with obtuse tooth at middle, corolla 6–10 mm diam. **Notechidnopsis**
3. Tubercles on stem arranged into 4–5 angles 11.
11. Stems, pedicels, sepals and outside of corolla at least finely pubescent (stems sometimes nearly glabrous), leaf-rudiments deciduous, erect (except *S. engleriana*), corolla often covered inside with fine slender hairs **Stapelia**
11. Stems, pedicels, sepals and outside of corolla glabrous, leaf-rudiments spreading or absent 12.
12. Inflorescences produced in upper half of stem, usually several per stem 13.
13. Outer corona much reduced to absent (as spreading lobe beneath guide-rails), deep nectarial cavity present beneath guide-rails **Piранthus**
13. Outer corona not much reduced, nectarial cavity shallow or absent 14.
14. Young tubercle tipped with leaf-rudiment constricted slightly at base above tubercle 15.
15. Surface of stem smooth, corolla inside covered with papillae, corolla lobes not crested along middle **Australiuma**
15. Surface of stem rugulose, corolla without papillae, corolla lobes crested along middle **Baynesia**
14. Young tubercle either without leaf-rudiment or with tubercle continuing (without constriction) into leaf-rudiment 16.
16. Tubercle obtuse and not tapering to an acute or acuminate tip 17.
17. Plant shrub-like and rooting on central stem only, flowers arising in several clusters, often in vertical series in grooves on opposite sides of stem, without peduncle, flowers in cluster opening = simultaneously, corona 2–3 mm broad, pollinia broader than long **Quaqua**
17. Plant clump-forming or rhizomatous and rooting on many side-branches, flowers arising in 1–several scattered inflorescences and opening in gradual succession, often developing small peduncle, corona 4–11 mm broad, pollinia longer than broad **Tromotriche**
16. Tubercles not obtuse, tapering into acute to acuminate (sometimes soft to hard spike-like) leaf-rudiment 18.

(continued on next page)

Key to the Genera of Stapeliads in Southern Africa and Madagascar (continued)

16. Stems hard, surface micro-papillate (dull and not shiny), tubercle tapering into hardened tooth-like to spike-like leaf-rudiment, flowers arising in several clusters, often in vertical series in grooves on opposite sides of stem **Quaqua**
18. Stems soft, surface smooth ($\pm$ shiny), tubercle tapering into soft tooth-like leaf-rudiment, flowers arising in 1-several scattered inflorescences **Orbea**
12. Inflorescences arising in lower half of stem, usually only 1 per stem **19.**
19. Surface of stems with raised longitudinal ridges, gynostegium dominated by comparatively large discrete dorsiventrally flattened ascending to erect (spreading in *S. arenarius*) outer corona lobes forming cup around small inner lobes (these adpressed to backs of anthers and rarely exceeding them), anthers and pollinia descending slightly towards centre of somewhat concave style head (plants from Madagascar) **Stapelianthus**
19. Surface of stems without raised longitudinal ridges, outer corona lobes not as above, anthers and pollinia horizontal or ascending towards centre of flat to convex style head (plants not from Madagascar) **20.**
20. Inner corona lobes laterally flattened, rising above anthers and connate in centre well above style head **Stapeliopsis**
20. Inner corona lobes dorsiventrally flattened and adpressed to backs of anthers for most of their length **21.**
21. Stems hard, surface micro-papillate (dull and not shiny), tubercle tapering into hardened tooth-like to spike-like leaf-rudiment, flowers arising in several dense clusters, often in vertical series in grooves on opposite sides of stem (opening $\pm$ simultaneously in each cluster) **Quaqua**
21. Stems comparatively soft, tubercles tipped with soft leaf-rudiment or none present, flowers usually in single inflorescence per stem and mainly solitary **22.**
22. Tubercles > 2 mm long and clearly raised out of surface of stem, corona > 3 mm tall, pollinia comparatively large (> 0.4 mm long) **23.**
23. Surface of stems micro-papillate (dull and not shiny), tubercles obtuse and not tapering to tip, leaf-rudiment $\pm$ absent **Tromotriche**
23. Surface of stems smooth ($\pm$ shiny), tubercles not obtuse, tapering into leaf-rudiment, leaf-rudiment present **24.**
24. Leaf-rudiment deltoid to subulate, slightly constricted at base, caducous, with small multicellular hairs in stipular position and along margin but lacking stipular denticles, corolla usually covered with multicellular papillae **Tridentea**
24. Tubercle tapering $\pm$ uniformly to tip and leaf-rudiment without basal constriction, without small hairs in stipular position but frequently with stipular denticles, corolla from deeply rugulose to smooth but rarely with multicellular papillae **Orbea**
22. Tubercles < 1 mm long and scarcely raised out of surface of stem, corona < 1.5 mm tall, pollinia minute (< 0.2 mm long) **Ophionella**

1. Australluma



Australluma Plowes, *Haseltonia* 3: 54 (1995).
Type: *A. peschii* (Nel) Plowes.

Dwarf spineless highly rhizomatous succulent forming small clumps to 30-100 mm diam. connected by underground rhizomes up to 300 mm long, rarely mat-forming. Stems 50-150 mm long, 3-5 (-10) mm thick, erect from horizontal underground rhizomes (up to 200 mm long) to nearly prostrate and without any underground rhizomes, fleshy and firm, glabrous, silvery grey-green to dark brown, often finely mottled with purple; *tubercles* 2-4 mm long, hardly rising from surface of stem, rectangular in outline, joined into 4 obtuse angles along stem with slight $\pm$ continuous shallow grooves between them; *left-rudiment* 0.5-5 mm long, ascending to spreading, subulate to deltoid, acute, inserted just below base of next tubercle, usually subtended by 2 erect obtuse stipular denticles. *Inflorescences* glabrous, 1-10 per stem, arising in upper half, each bearing 1-3 flowers, peduncle short to abscond, with 1-3 deltoid bracts < 1 mm long without lateral teeth; *pedicel* 1-7 mm long, 1.0-1.5 mm thick, descending to erect; *sepals* 1.5-4 mm long, 1 mm broad at base, ovate-lanceolate, acute to acuminate. *Corolla* 7-17 mm diam. rotate, deeply lobed: outside smooth and glabrous; inside red to brown or yellow-green, smooth to rugulose, on lobes and to just below their base covered with small mound-like papillae each with an enlarged apical cell; *tube* 0.5-1 mm deep, shallowly consisting of 2 closely intergrown series of lobes arising blow-shaped, surrounding lower part of gynostegium; *lobes* 3-7 mm long, 2-4 mm broad at base, spreading, ovate-deltate, acute, upper surface convex from recurved eciliate margins. *Corona* 1.5-2 mm tall, 2.5-5 mm broad, consisting of 2 closely intergrown series of lobes arising on staminal tube, glabrous, with very slight basal stipe to senile; *outer lobes* forming $\pm$ continuous cupular stricture around gynostegium, bifid in middle and shortest opposite guide-rails and longest (at 1-1.5 mm) behind after, somewhat cupular beneath guide-rail; *inner lobes* 0.5-1.0 mm long, adpressed to backs of anthers, shorter than anthers to meeting in centre, dorsiventrally flattened, obtuse, subulate to rectangular. *Anthers* horizontal on top of style-head, margin often not shrinking back and covering pollina, $\pm$ semicircular. *Pollinum* $\pm$ D-shaped insertion-crest exactly along outer edge, caudicle attached with small circular pad to ventral surface. *Follicles* erect, terete-fusiform, obclavate, slender, consisting of 2 horns diverging at 30-60°, longitudinally mottled with narrow broken purple strips, glabrous, smooth.

The name *Australluma* was coined for the one species of *Caralluma* that is endemic to Namibia.

Caralluma was established in 1810 by Robert Brown for the species from India described by Roxburgh as *Stapelia adscendens*. Haworth (1812) moved it *Stapelia* into *Caralluma* and also described *Caralluma umbellata*, so that at that stage there were only two species known. With the botanical exploration of Indian gaining new impetus from the efforts of Wight, Amot and many others, further species came to be known from there. These were initially placed in two other genera, *Boucerosia* and *Hutchiana*, which were both described by Wight and Amot in 1834. Decaisne (1844) placed some of these species in *Boucerosia* and some in *Desmidorchis*. N.E. Brown (1890; 1892) decided that all these genera were impossible to separate and that the species all belonged under *Caralluma*. By this time a considerable number of species had been described and consequently *Caralluma* became very large. White & Sloane (1937) kept largely to Brown's generic concepts and their account of *Caralluma* contained 105 species (and a few extra ones listed at the end), which made it the largest genus of stapeliads by a considerable margin.

Since 1978, *Caralluma* has been steadily reduced in size. This process began when L.C. Leach moved several species to *Orbea*, *Orbeopsis* and *Pachycymbium*. Gilbert (1990) continued this process, moving many more species of *Caralluma* from both north-east Africa, Arabia and southern Africa to *Pachycymbium* and leaving 56 species in *Caralluma*, of which only a single species, *C. peschii*, occurred in southern Africa. He divided *Caralluma* into four subgenera but did not actually revise the genus. Plowes (1995b) also attempted to subdivide *Caralluma*, breaking it into 17 genera of which six are monotypic, again without revising the genus. This arrangement has not met with much enthusiasm. However, molecular evidence (Meve & Liede 2002) shows that *C. peschii* is not related to the other species of *Caralluma*. This suggests that its segregation into a separate genus, *Australluma*, is justified. In Meve & Liede (2002, fig. 4) this species occupied an unresolved position among the most derived stapeliads. Our own studies have shown that it forms a branch with *Orbea ubomboensis* that is strongly supported and is sister to a group containing *Orbea* and *Tavaresia*. *Orbea ubomboensis* is therefore also moved to *Australluma*, which now contains two species and is closely allied to *Orbea*.

Orbea ubomboensis has proved to be a difficult species to place. The uniformly darkly coloured, small flowers are more similar to those of the species of *Orbea* from north of the equator, but the stems are, on the other hand, different from those in any of these species. The treatment in Bruyns (2002) placed it at the base of *Orbea* along with *O. schweinfurthii*, but there was no statistical support for this arrangement, in contrast to the present arrangement, for which the statistical support is strong.

Australluma is defined by the slender and soft, highly rhizomatous stems with small, distinctly defined leaf-rudiments, usually with tiny stipular denticles near their bases. The flowers are small and borne in numerous small inflorescences towards the tips of the stems. On the inside they are rugulose *A. ubomboensis* but in both species the surface is covered with small papillae with an enlarged apical cell that is particularly noticeable in *A. peschii* (fig. 27 E). The gynostegium is low, with broadly diverging and deeply bifid outer corona lobes and flat inner lobes that just cover the anthers.

1. *Australluma peschii*

Australluma peschii (Nel) Plowes, *Haseltonia* 3: 54 (1995).
Caralluma peschii Nel, *Jahrb. Deutsch. Kakteen-Ges.* 1 (6): 41 (1935).
Type: Namibia, Omaruru, *Pesch* sub STE 7082 (BOL).

Dwarf spineless highly rhizomatous succulent forming small clumps to 80 mm diam., with rhizomes up to 300 mm long. Stems 40-150 mm long, 3-5 (-8) mm thick, erect from horizontal underground rhizomes (up to 200 mm long) fleshy and firm, glabrous, silvery grey-green finely mottled with purple, *tubercles* < 2 mm long, hardly rising from surface at stem, rectangular in outline, joined into 4 obtuse and obscure angles along stem with slight $\pm$ continuous shallow grooves between them, *left-rudiment* $\pm$ 2 mm long, 1.5 mm broad at base, ascending persisted, subulate, acute, inserted just below base of next tubercle, subtended by 2 erect obtuse stipular denticles. *Inflorescences* glabrous, 3-10 per stem, arising in upper half, each bearing 1-2 flowers, without peduncle, with 1-3 deltoid bracts < 1 mm long without lateral teeth; *pedicel* 1-2 mm long, 1.0-1.5 mm thick, descending and holding flower facing partly downwards, usually somewhat longitudinally ridged; *sepals* 2-4 mm long, 1 mm broad at base ovate-lanceolate, acute. *Corolla*

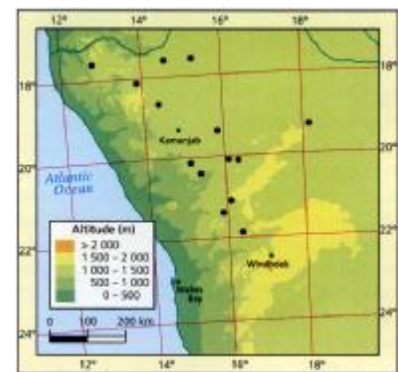


Fig. 1.1. Distribution of *Australluma peschii*.

Australluma peschii

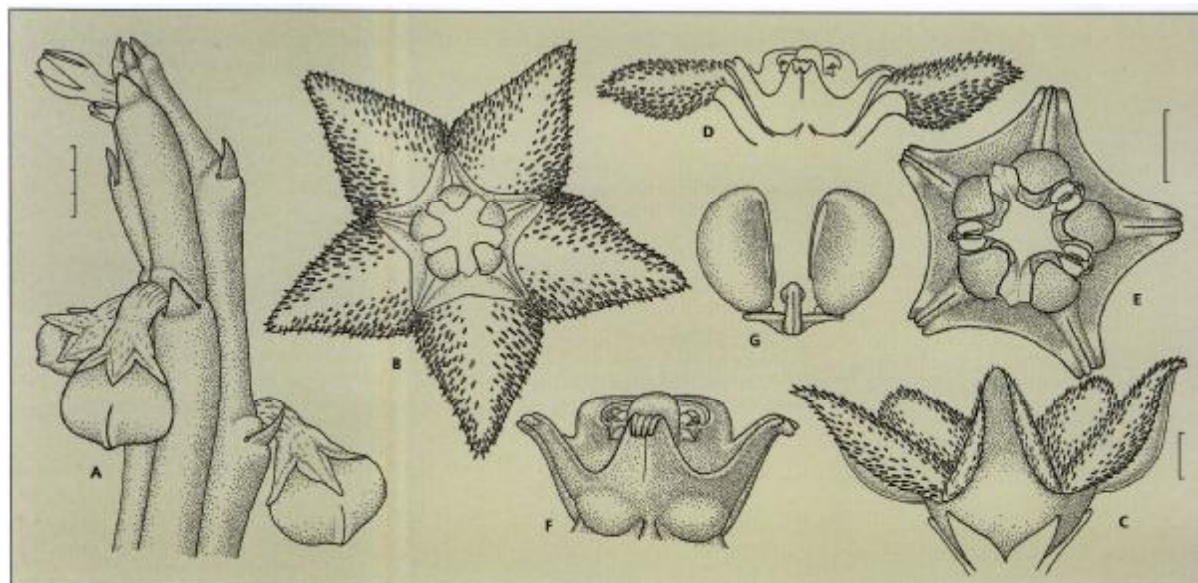


Fig. 1.2. *Australluma peschii*. **A**, apex of stem with several buds. **B**, faces view of flower. **C**, side view of flower. **D**, side view of dissected flower. **E**, faces view of gynostegium. **F**, side view of gynostegium. **G**, pollinarium. Scale bars: A, 3 mm; B-D, 1 mm (at C); E, F, 1 mm (at E); G, 0.25 mm (at E). Drawn from: PVB 2345, Omaruru Townlands, Namibia.

9-10 mm diam, rotate, deeply lobed; outside smooth and glabrous, pale green to brownish; inside on lobes and to just below their bases covered with small columnar papillae each with a cylindrical transparent ± obtuse apical cell, yellow-green sometimes suffused with red; tube ± 1 mm deep, shallowly bowl-shaped, surrounding lower part of gynostegium; lobes 3.5-5.0 mm long, 2-3 mm broad at base, spreading, ovate-dictate, acute, upper surface convex from recurved eciliate margins. Corona ± 2 mm tall, 4 mm broad, consisting of 2 closely intergrown series of lobes arising on staminal tube, glabrous, with very slight basal stipe to sessile; outer lobes forming apparently ± to brown around edges tending to pale yellow towards base, broadly bifid so as to be shortest opposite guide-rails and longest (at nearly 1 mm) behind anther, somewhat cupular beneath guide-rail; inner lobes 0.5-0.7 mm long, adpressed to backs of anthers, shorter than anthers to meeting in centre, dorsiventrally flattened, obtuse, subulate to rectangular, pale yellow often with red to brown margins.

Distribution and habitat

Australluma peschii has been found widely in the tropical parts of Namibia between Okahandja and Etosha National Park as well as north of this in the Kaokoveld between Opuwa and Van Zyl's Pass and in Ovamboland. It has also been collected north of Grootfontein and this leads one to suspect that it is considerably more widely distributed than was indicated in Bruyns (1982c). However, there is still no evidence that it is not endemic to Namibia.

A. peschii occurs mostly in fairly dry areas, though it does not venture into the Namib

Desert. It usually grows in small bushes (frequently the acanthaceous shrub *Monechma cleomoides* (*M. arenicola*) or in grass tufts among scattered small *Acacia* trees. Plants usually grow right inside the bush, with the stems mingling with those of the bush itself. This makes them remarkably inconspicuous, since their grayish colour closely matches that of the bark of the bush's stems.

Diagnostic features and relationships

This species is particularly odd because of its soft, slender stems which do not generally exceed 5 mm in thickness and because it forms small clusters. The underground rhizomes connecting these clusters may be anything up to 200 mm long and may also be somewhat thicker than those above the surface. In habitat the above-ground parts are usually silvery grey with fine longitudinal darker markings and this colouring blends in very well with the stems of the bush inside which the plant is growing. In cultivation they often tend to be greener. These stems are edible when turgid and have a slightly sourish but not unpleasant taste combined with a lettuce-like consistency. Tubercles are present all along the stems but are low and rounded so that the stem is only obscurely 4-angled. At the top of each tubercle, just below the beginning of the next one, there is a small, deltoid left-rudiment that persists some time before drying out.

Flowers arise in the upper half of the stems

on numerous small inflorescences. Each inflorescence lies at the top of a tubercle and is situated just adjacent to the left-rudiment. Most of them produce one or occasionally two flowers on short, descending, relatively stout and often somewhat longitudinally fluted pedicels.

The somewhat plain flowers are small (at 9-10 mm diameter) and face slightly downwards. They are more or less flat with a small, bowl-shaped depression in the centre which contains the lower half of the gynostegium. Generally the inside is pale yellowish to faintly greenish, but in the Kaokoveld from around Opuwa to Van Zyl's Pass it is usually spotted with red on a yellowish background. On the lobes and up to the mouth of the tube the inside is covered with small, multicellular papillae and each of these has a much enlarged apical cell, which is cylindrical and transparent and up to two or three times the length of the papilla. These give the inner surface the appearance of being hairy.

The gynostegium is almost sessile and somewhat broader than tall. On a superficial examination the outer coronal series appears to be continuous around the gynostegium, with five spreading truncate teeth behind the inner lobes connected by a narrower band of tissue opposite the guide-rails. If these teeth are examined closely they will be seen to consist of part of two adjacent lobes pressed tightly together and partly fused. That they are made up from the spreading parts of adjacent outer lobes is confirmed by following their development which shows that the outer lobes develop more along their margins than in their middle and spread out

to become contiguous behind the inner lobes. Each outer lobe is somewhat swollen basally to form a cup-like bay beneath the guide-rail and has a hidden nectarial cavity there as well. The inner lobes small and adpressed to the anthers, sometimes exceeding them to meet in the centre.

History

Australluma peschii was discovered by Carl Peter Paul Pesch (1876–1970) near Omaruru in central Namibia. Pesch was a typist in Omaruru from 1909 until 1915 and after World War I became Town Clerk of Omaruru. His son Heinz Hans Pesch went to work with H. Herre and G.C. Nel at the Botanical Garden of the University of Stellenbosch for two years beginning in 1933 (P. Craven, pers. comm. 2000). It seems most likely that he took material of this species that his father had found with him and thereby brought it to their notices.

The *Jahrbuch der Deutschen Kakteen-Gesellschaft*, in which this and several other stapeliads were published by G.C. Nel, appeared in 18 monthly installments between July 1935 and December 1936 (U. Eggli, pers. comm. 2000). It is therefore reasonable to assume that *A. peschii*, which appeared in the sixth of these installments, was published in December 1935 and not in 1936 as is usually assumed.



Fig. 1.3. *A. peschii*, PVB 5498, north of Grootfontein, Namibia.



Fig. 1.4. *A. peschii*, PVB 8054, near Vanzyl's Pass, Namibia, with speckled flowers.



Fig. 1.5. *A. peschii*, PVB 7991, east of Opuwa, Namibia. A medium-sized plant about 6 cm tall among dead twigs, in habitat, December 1999.

2. *Australluma ubomboensis*

Australluma ubomboensis (L. Verd.), Bruyns

comm. nov.

Caralluma ubomboensis L. Verd., Fl. Pl. South Africa

12: t. 443 (1932).

Pachycymbium ubomboensis (L. Verd.) M.G. Gilbert, *Bradleya* 8: 25 (1990).

Angolluma ubomboensis (L. Verd.) Plowes, *Excelsa* 16: 119 (1994).

Orbea ubomboensis (L. Verd.) Bruyns, *Aloe* 37: 76 (2001).

Type: South Africa, Natal, Lebombo Mountains, Pole Evans sub PRE 8764 (PRE).

Dwarf succulent usually consisting of several very small clumps of stems 30–100 mm diam., connected by underground rhizomes or mat-forming. Stems 15–80 mm long, 4–10 mm thick, slender, erect from underground rhizomes (up to 150 mm long) to nearly prostrate and without any underground rhizomes, uniformly dark green to dark grey or dark brown occasionally mottled with darker brown; tubercles 2–4 mm long, few, very obscure and joined into 4 obtuse angles along stem with slight groove between angles, with short spreading deltoid tooth (< 1 mm long) near upper end, flattened above and occasionally with 2 small stipular denticles on either side near base. Inflorescences 1–3 per stem near apex, each of 1–3 flowers developing in gradual to rapid succession from



Fig. 1.6. Distribution of *Australluma ubomboensis*.

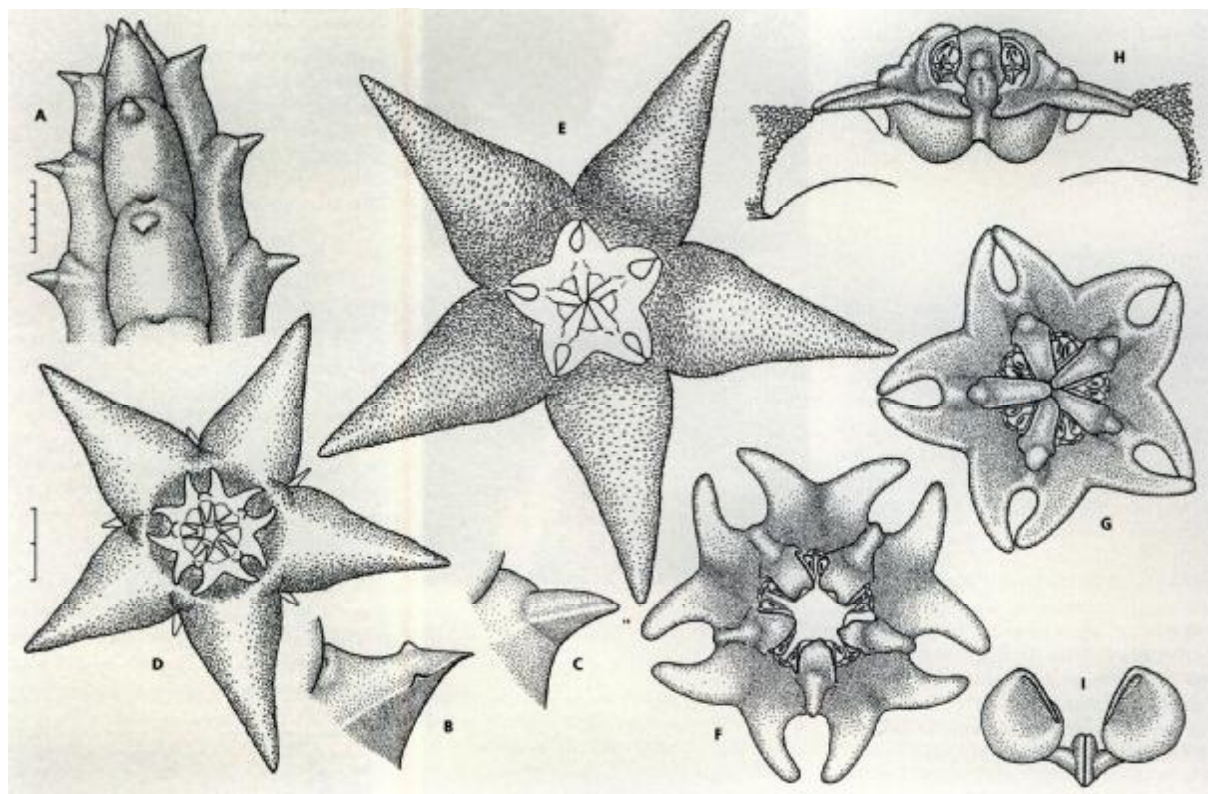


Fig. 1.7. *Australluma ubomboensis*. A, apex of stem. B, C, apex of tubercle. D, E, face view of flower. F, G, face view of gynostegium. H, side view of centre of dissected flower. I, pollinarium. Scale bars: A, 5 mm; B, C, F-H, 1 mm (at D); D, E, 2 mm (at D); I, 0.25 mm (at D). Drawn from: A, C, PVB 7471, Nzhelele, near Messina; B, E, G, I, PVB 4455, Ubombo; D, Hardy 5409, Mutale Gorge, Pafuri; F, H, hort. F. Noltee.

short peduncle (< 5 mm long); *pedicels* 1-7 mm long, 1 mm thick, erect; *sepals* 1.5-2.0 mm long, 1 mm broad at base, ovate-lanceolate, acuminate. *Corolla* 7-17 mm diam., rotate, deeply lobed; outside smooth, pale cream-green to purple-brown and 2-3-veined down each lobe; inside red or maroon to dark purple-brown, sometimes white around gynostegium, deeply to finely transversely rugulose and papillate over whole surface; tube $\pm$ 0.5 mm deep, containing lower half of gynostegium, with corolla somewhat thickened around mouth; *lobes* 3-7 mm long, 2-4 mm broad at base, spreading to recurved, deltate to ovate, acute, convex from reflexed eciliate margins. *Corona* 1.5 mm tall, 2.5-5.0 mm broad, raised above base of tube on short pentagonal stipe (< 0.5 mm long); *outer lobes* 1.0-1.5 mm long, spreading to touch surface of corolla at mouth of tube, bifid nearly to base into dorsiventrally flattened linear diverging obtuse lobules, with low flattened ridge joining adjacent lobes behind anthers, dark purple-brown becoming red towards base or wholly maroon; *inner lobes* 0.5-1.0 mm long, adpressed to backs of anthers and sometimes exceeding them to meet in centre, dorsiventrally flattened, linear, obtuse to truncate-emarginate, white with reddish margins to wholly maroon.

Distribution and habitat

Since its discovery, *A. ubomboensis* has been gathered particularly in that part of the Lebombo (Ubombo) Mountains that lies alongside the Swaziland border in the territories of KwaZulu-Natal, Moçambique and Swaziland, roughly between the towns of Ubombo in KwaZulu-Natal and Goba in Moçambique. It is also known in the extreme north-eastern corner of South Africa between Wyllie's Poort and Pafuri,

and it continues northward from this area into eastern Zimbabwe at least as far north as Gutu and near Chipinga. A recent record was also made in coastal Moçambique north of the Save River, more than 800 km from the only other known collections from Moçambique (from the vicinity of Goba on the eastern flank of the Lebombo Mountains). This gives it a very wide and diffuse distribution, but the plants are generally extremely insignificant and therefore may be easily overlooked. Thus it may eventu-



Fig. 1.8. *A. ubomboensis*, PVB 4455, Ubombo.



Fig. 1.9. *A. ubomboensis*, PVB 8750, north of Save River, Sofala Province, Mozambique.

ally prove to be more common than the few records indicate.

Australluma ubomboensis occurs in a wide variety of habitats, usually on rock outcrops on hills or mountains. It may occur in seasonally quite wet areas as, for example, around Ubombo where plants grow in shallow pockets of soil in crevices on rock outcrops with *Xerophyta* and *Aloe vanbalenii*. In the area north of the Soutpansberg it is found in dry and fairly open 'forests' of *Androstachys johnsonii* among rocks on the slopes of hills. It occurs in crevices on granite domes near Gutu in Zimbabwe, together with *Euphorbia tortistyla*, *Anacampseros rhodesica*, *Selaginella* and *Myrothamnus*. In Mozambique north of the Save River (at an altitude of about 70 m) it was found to be locally very common in dry woodland consisting of *Acacia nigrescens*, *Commiphora* and *Gardenia* among others, growing in leaf-litter on pale sands.

Diagnostic features and relationships

Although they may reach a length of 80 mm in cultivation, in the field stems of this species are small, often only 20 mm tall and 5 mm thick. The plants form small clumps (often as small as 20-40 mm in diameter) which may be connected beneath the surface by slender white runners up to 150 mm long. These runners increase 2-4 times in thickness on emerging from the soil. Plants found recently north of the Save River in Mozambique showed no evidence of subterranean growth at all, with the small stems spreading nearly horizontally on the surface of the soil, as is usually seen in *Orbea schweinfurthii*, but this is the only locality where such a habit has been seen. The above-ground portions are usually dark green or dark grey



Fig. 1.10. *A. ubomboensis*, PVB 7471, Nzhelele, near Messina.

to brown and relatively rarely have a darker mottling. The tubercles are low and obscure, and each is tipped (near the Base of the next tubercle) with a very short deltoid tooth that is noticeably flattened above.

Flowers are produced mainly on young growth on a few small inflorescences near the apices of the stems. The pedicels are short and hold the flower facing upwards, but close to the stem. Florally this is not an imposing species but, for their size, the flowers emit quite a strong, slightly fruity, foetid smell. In cultivation numbers of tiny flies (3-4 mm long) have been seen swarming over the flower shortly after it has opened and these have been observed to remove pollinia. The flowers are small and fairly deeply lobed, with only a small united portion around the corona, and they are either more or

less flat or have somewhat reflexed lobes. Inside they are dark purple-brown to maroon or even red. There is often a slightly paler medial patch radiating along each lobe. The inside is velvety in appearance and under the microscope this can be seen to come from a dense covering of irregularly transverse ridges which are themselves finely papillate (fig. 29 C, D).

The corona is small, fitting closely into the tiny tube and just slightly projecting from it to form a low cushion in the centre of the flower. The deeply bifid and widely diverging outer lobes are adpressed to the corolla and have a similar colour. They usually glisten over much of their upper surface with small pools of nectar. The inner lobes are adpressed to the anthers and vary from white to maroon.

Although Leach (1978a) suggested that this species is allied to *Orbea miscella*, this has not been substantiated by recent studies. In Bruyns (2002) it was found to be closest to *O. schweinfurthii*, but again this has not been confirmed by further work, which clearly places it with *A. peschii*.

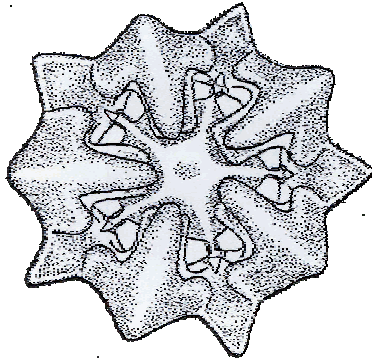
History

The 'Ubombo *Caralluma*' was discovered by I.B. Pole Evans in the KwaZulu-Natal part of the Lebombo Mountains and seems to have flowered in cultivation for the first time in February 1930. It was also recorded in 1935 for the first time by Donald R. Keith in Swaziland. *Australluma ubomboensis* was first located in Mozambique by A. Esteves de Sousa in March 1945 (Gomes e Sousa & Esteves de Sousa 1947) and he collected it with other succulents among rocks at Goba, which lies along the eastern slopes of the Lebombo Mountains. In Zimbabwe it seems to have been discovered by L.C. Leach in 1964.



Fig. 1.11. *A. ubomboensis*, PVB 7471, Nzhelele, near Messina, flowers with a more reddish colour than usual.

2. Baynesia



Baynesia Bruyns, *Novon* 10: 354 (2000).
Type: *Baynesia lophophora* Bruyns.

This monotypic genus was erected to accommodate a species that was recently discovered in the north-westernmost corner of Namibia. In this species there are so many unusual features both in the vegetative parts and in the flowers that it was not possible to accommodate it in any of the previously recognised genera.

Particularly unusual in this very anomalous species is the rugulose surface of the stems; this is unlike any other in southern Africa. Rugulose stem-surfaces are found in *Echidnopsis leachii* from Tanzania (Bruyns 1988) and the surface is longitudinally bullate in most species of *Stapelianthus* and in *Rhytidocaulon* (Bruyns 1999g). The surface is more regularly divided into raised polygons in *Pseudolithos* and *Anomalluma* (Bruyns & Meve 1995) and it is, in fact, to *A. dodsoniana* that this new species bears a considerable likeness. This likeness continues into the epidermal cells on the stems, which also have their outer walls raised into papillae in *Baynesia*. The leaf-rudiments in *Baynesia* are larger than those of any *Pseudolithos* and occasionally have small stipular denticles, which are never found in *Pseudolithos*.

The 4-angled stems with many small inflorescences near their apices and the small flowers all suggest a relationship with *Cara-luma*, whose species are all found north of the equator. Whereas in *Caralluma* there is a wide variety of corolla forms and coronal structures, the curiously ridged and papillate, crested corolla lobes in *B. lophophora* are unique. The stems in *Caralluma* are neither rugulose nor papillate. Leaf-rudiments are always present in *Caralluma* and stipular denticles are nearly always present. In addition, in most species of *Caralluma* there are many small translucent hairs on the margins of the leaf-rudiments and around the stipular denticles, but these are not found in *Baynesia*.

Characters of the pollinaria have often proved helpful for delimiting the genera of the

stapeliads (Gilbert 1990; Meve 1994; Bruyns & Meve 1995; Bruyns 1995a; 1999g). Those of *B. lophophora* are particularly unusual. Whereas the pollinia in *Caralluma* may be broader than long, in *B. lophophora* they are exceptionally broad and have remarkably minute caudicles and wings on the corpuscles. This is again unmatched anywhere either in *Caralluma* or in *Pseudolithos*.

Our own molecular researches have not clarified the relationships of this remarkable species. However, they have served to show that it is not closely allied to any species of *Anomalluma*, *Caralluma*, *Echidnopsis*, *Pseudolithos* or *Rhytidocaulon* nor is it closely allied to any of the other genera with small flowers in southern Africa either.

Baynesia lophophora

Baynesia lophophora Bruyns, *Novon* 10: 354 (2000).

Type: Namibia, Kaokoveld, Baynes Mountains, Bruyns 8000 (BOL, holo.; K, MO, PRE, WIND, iso.).

Dwarf spineless non-rhizomatous succulent forming clumps 30-80 (-150) mm diam. Stems 30-80 mm long, 6-12 mm thick, erect, fleshy and fairly soft, glabrous, somewhat transversely rugulose and finely papillate, green to suffused with brownish; tubercles obscurely conical, slightly spreading, laterally flattened and fused into 4 obtuse and obscure angles along stem with concave area between them; leaf-rudiment 1.0-1.5 mm long, spreading, caducous, cordate-acute, inserted just below base of next tubercle, with very occasional stipular denticles. Inflorescences glabrous, usually 3-10 per stem, arising towards apex, each bearing 1-3 (-5) flowers developing in gradual succession, without peduncle, with minute linear bracts < 1 mm long without lateral teeth; pedicel 1.5-2.5 mm long, < 1 mm thick, descending and holding flower facing partly downwards, usually somewhat longitudinally ridged, reddish; sepals $\pm$ 1.5 mm long, 0.5 mm broad at base, lanceolate, acuminate. Corolla 3-4 mm long, 6-8 mm broad, campanulate, shallowly lobed; outside smooth and glabrous, pale green suffused with

red; inside deep maroon becoming cream in lower half of tube, glabrous, papillate only in two lines along edges of fold in lobes ($\pm$ around mouth of tube); tube $\pm$ 1.5 mm long, 3-4 mm broad at mouth, $\pm$ hemispherical; lobes $\pm$ 2 mm long, 2 mm broad at base, erect, ovate-acute, folded along midrib so that inside crested towards apex, apex recurved, margins eciliate. Corona $\pm$ 1 mm tall, 2 mm broad, consisting of 2 series of lobes arising on staminal tube and partly intergrown, glabrous, with very short basal stipe; outer lobes $\pm$ 0.5 mm long and broad, deltoid, acute, spreading, dark maroon in patch beneath guide-rail otherwise transparent, laterally fused to bases of inner lobes towards base; inner lobes $\pm$ 0.5 mm long, adpressed to backs of anthers and mostly equaling them, dorsiventrally flattened and slightly convex above, obtuse, with obtuse swollen dorsal projection between outer lobes, cream. Anthers horizontal on top of style-head, margins shrinking back to expose pollinia, rectangular. Pollinium ellipsoidal, much broader than long, insertion-crest exactly along outer edge, caudicle attached with small circular pad to ventral surface. Follicles 25-35 mm long, 2.5-3.5 mm thick, erect, terete-fusiform, obclavate, slender, consisting of 2 horns diverging at 30-60°, faintly streaked with brown on cream-green, glabrous, smooth.

Distribution and habitat

This new species is, at present, known only from the north-facing aspects of the higher parts of the Baynes Mountains overlooking the Kunene River in the north-western corner of Namibia. Here it occurs at an altitude of 1500-1600 m just above large, sandstone cliffs that dominate the landscape.

The vegetation of these cliffs is quite different from that of the surroundings and consists mainly of succulents. Species such as *Aloe corallina*, *Cotyledon orbiculata*, *Euphorbia otjipembana* and *Sarcostemma viminalis* are common and *Adenium obesum*, *Crassula tabularis* and *Stapelia schinzii* var. *angolensis* also occur, though more sporadically. On the relatively flat summits of these mountains the vegetation is practically devoid of succulents, being dominated by short trees and a thick cover of grass in years of reasonable rainfall. Immediately above the cliffs there is an apparently quite dry, rocky, transitional fringe with very shallow soils. This is covered with short tufts of grass and scattered *Petalidium* shrublets and there are occasional specimens of *Euphorbia otjipembana*, *E. mauritanica*, *E. monteiri* and *Stapelia schinzii* var. *angolensis*. It is in this transitional fringe that *B. lophophora* occurs and here it is quite common, with the plants usually well concealed under tufts of grass.

Diagnostic features and relationships

Plants of *Baynesia* are mostly small and consist of a cluster of erect stems. The four-angled, greenish stems are comparatively soft and have a rugulose surface that is also covered with fine

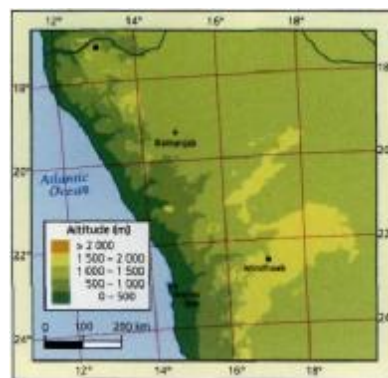


Fig. 2.1. Distribution of *Baynesia lophophora*.

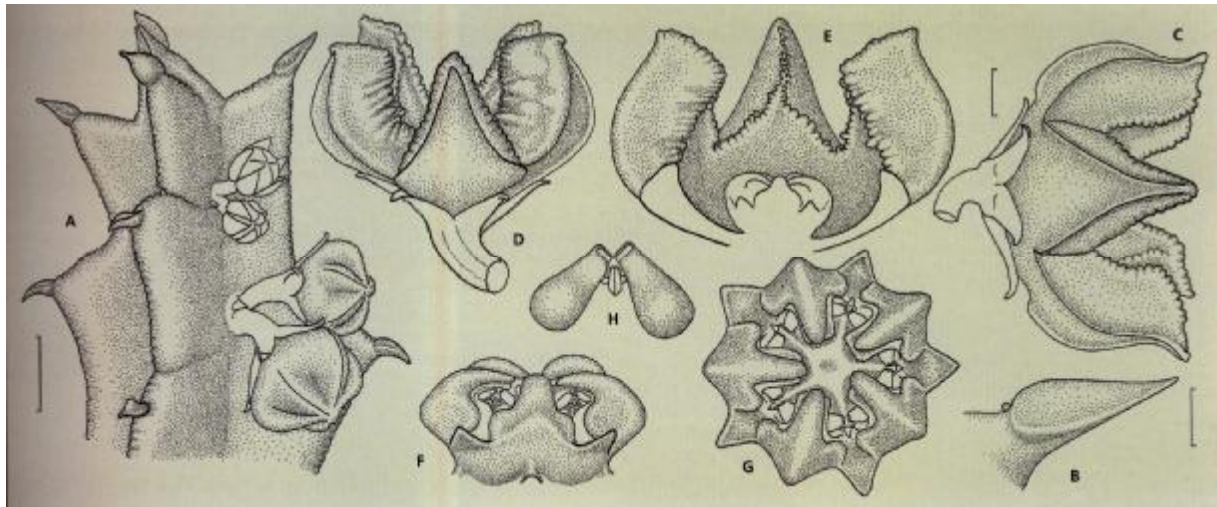


Fig. 2.2. *Baynesia lophophora*. A, apex of stem. B, side view of leaf-rudiment. C, D, side view of flower. E, side view of dissected flower. F, side view of gynostegium. G, face view of gynostegium. H, pollinarium. Scale bars: A, 2 mm; B, F, G, 0.5 mm (at B); C, D, 1 mm (at C); E, 1 mm (at B); H, 0.25 mm (at A). Drawn from: PVB 8000, Baynes Mountains, Namibia.

papillae. Each of the obscure tubercles bears a leaf which soon falls off. Stipular denticles are very intermittently present and there is often only one per tubercle, while most tubercles have none at all.

Flowers are borne in small clusters around the tips of the stems on new growth. They are small and nodding and emit a faint but still detectable, excrement-like odour for a short while after opening. Inside they are deep maroon on the lobes changing to cream in the

tube. The tube is more or less, hemispherical and the lobes are erect around its mouth. Each lobe has its margins quite well folded back and there is a peculiar ridge of papillae running along either side of the innermost surface from the mouth of the tube towards its apex. This makes the lobe appear to be crested on the inside and this crest is somewhat emphasised by the strongly recurved apices of the lobes.

The particularly small corona is very slightly raised above the base of the tube. The minute spreading outer lobes are transparent except for a dark maroon patch under the guide-rails, and the inner corona is cream but slightly more intense than the cream of the tube.

It is a remarkable fact that the tiny flowers of *Baynesia lophophora* are readily pollinated where I have them growing on a bedroom windowsill in Cape Town. This happens despite the fact that their natural habitat is more than 2 000 km away and it serves to demonstrate once again that many of these plants are not adapted to very localised pollinators.

History

This peculiar stapeliad was first observed on 15 December 1999 and I have been unable to find any other records of it. It is, however, not unlikely that similar plants occur in the very dry southern portion of Angola, where botanical exploration has been relatively superficial so far. Investigation of this region may therefore reveal that this species is not as isolated systematically as seems to be the case now. The generic epithet was chosen for the Baynes Mountains in the Kaokoveld of Namibia. These mountains were, in turn, named after an Englishman, Maudsley Baynes, who was commissioned by the Kaokoveld Land and Mining Company of London (to which the Kaokoveld was sold by the German Colonial Government) to explore the lower reaches of the Kunene River. This he did in 1911 and was the first European to investigate the area. It appears that the journey involved extreme hardship and that he only just survived it.



Fig. 2.3. *B. lophophora*, PVB 8000, Baynes Mountains, Namibia, showing nodding habit of flowers.

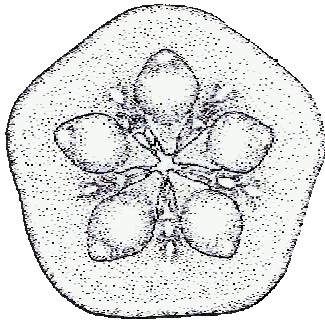


Fig. 2.4. *B. lophophora*, PVB 8000, Baynes Mountains, Namibia, portion of plant. The somewhat wrinkled surface of the stems is visible.



Fig. 2.5. *B. lophophora*, PVB 8000, Baynes Mountains, Namibia, showing clearly the pale colour of the inside of the flower and corona.

3. Duvalia



Haworth (1812) established the genus *Duvalia* for three species of *Stapelia* from the Cape of Good Hope which had been described by Masson a few years before (*S. caespitosa*, *S. elegans* and *S. reclinata*), as well as for *S. radiata* of Sims and several other species which he described himself. N.E. Brown revived the genus after some other authors, notably Decaisne (1844), had placed its species back in *Stapelia*. He moved several species to *Duvalia* and described some new ones.

White & Sloane (1937) recognised 15 species of *Duvalia*, of which all except *D. sulcata* (from Arabia) were from southern Africa. Since that time five more species were described from north-eastern Africa and Arabia and two new ones in southern Africa, so that altogether *Duvalia* contained 22 'species'.

In 1941 E.A. Bruce & P.R.O. Bally described *Duvalia tanganyikensis* from west of Mt Kilimanjaro in Tanzania. Two similar species, *D. andreaeana* and *D. procumbens*, were later also described. Bruce & Bally did not explain why their species was a *Duvalia*, possibly since the raised 'annulus' and narrow, spreading lobes were so suggestive of *Duvalia* that they felt the relationships were obvious. Bruce (1950) maintained that it was most closely related to *D. polita* and, although she mentioned that its growth habit was similar to that of *Huernia aspera*, the possibility that it could have belonged to *Huernia* does not seem to have been considered. Nevertheless, in due course this seems to have led to a useful re-examination of the criteria separating *Duvalia* and *Huernia*. Brown (1907-09) defined *Duvalia* and *Huernia* more precisely than had been done before. However, although he gave several characters which separated these genera, he actually

'keyed' them out by the presence (in *Huernia*) or absence (in *Duvalia*) of teeth on the corolla in the angles between the lobes. Emphasis on these teeth seems to have misled several later authors. This is unfortunate, since they are variably present in many genera of stapeliad and are not actually useful even for separating *Huernia* and *Duvalia* as they are known today, as Leach (1974a) pointed out. Leach (1969a; 1974a) gave a list of characters that were unique to *Duvalia* and of these

- (1) corolla lobes replicate (edges flat or folded upwards in *Huernia*)
- (2) corona with basal stipe (without basal stipe and $\pm$ adnate to base of corolla tube in *Huernia*)
- (3) leaf-rudiment with minute stipular denticles (stipular denticles absent in *Huernia*)

seem to be the most important. According to these criteria, the three previously mentioned species of *Duvalia* (*D. andreaeana*, *D. procumbens* and *D. tanganyikensis*) clearly belonged to *Huernia* and that is where they were transferred by Leach (1969a). Despite some rumblings of discontent (Dyer 1971), which were dealt with again (firmly!) by Leach (1974a), this is where these species have remained.

It has since been demonstrated that all the species of *Duvalia* in Arabia and north-eastern Africa lack any trace of stipular denticles (Meve 1997), so this character is not useful for separating these genera, except in southern Africa.

Furthermore, the figures that have been published of *H. procumbens* are not especially accurate and it has been found, on closer examination, that here, unlike in *H. tanganyikensis*, there is a short stipe beneath the outer corona lobes. The disc formed by these lobes rests on the side of the corolla tube, just as in *Duvalia*. While this stipe is not as long as in any other *Duvalia*, it is nevertheless present. A considerably longer stipe is present beneath the corona in *H. kennedyana*. Therefore, this character, too, is not unequivocal in separating the two genera, so Leach's opinion that *Duvalia* and *Huernia* 'may possibly prove to be the most distinctly differentiated in the whole tribe' (Leach 1969a) is rather too optimistic. Meve (1997) mentioned two further characters:

- (1) the guide-rails in *Huernia* are double, differentiated into an outer groove and an inner rail, while those in *Duvalia* are simple. Kunze (1982) is quoted as the authority for this.
- (2) the 'tubercle' on the outer coronal disc beneath the base of the guide-rail which obscures the mouth of the nectarial cavity in *Huernia* is lacking in *Duvalia*.

Actually Kunze (1982) examined the guide-rail rather informally in a single species of *Huernia* only, and did not look at it in *Duvalia* at all, nor

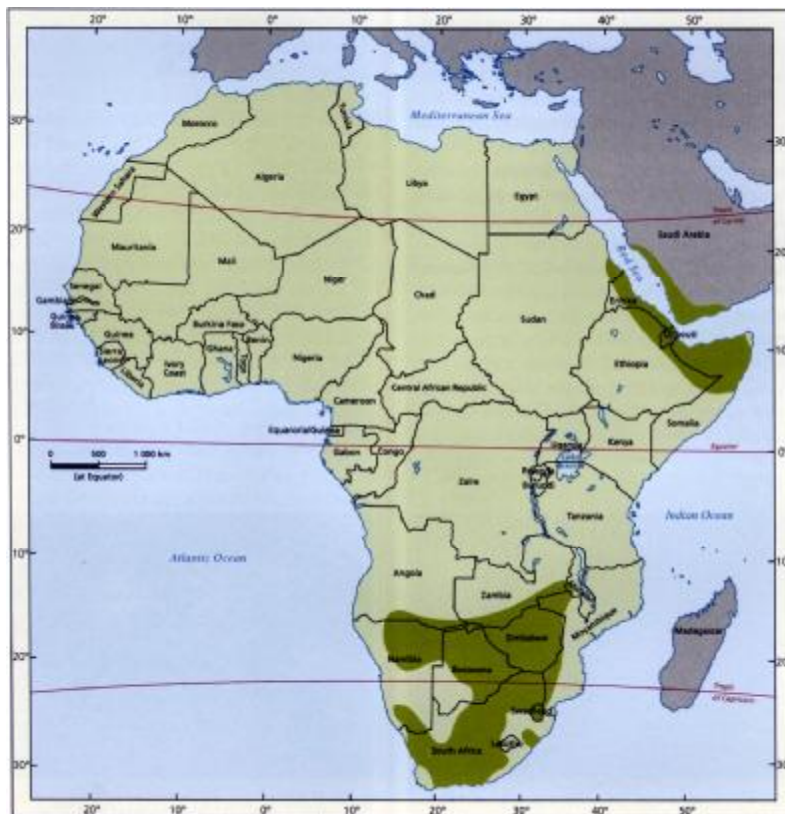


Fig. 3.1. Distribution of *Duvalia*.

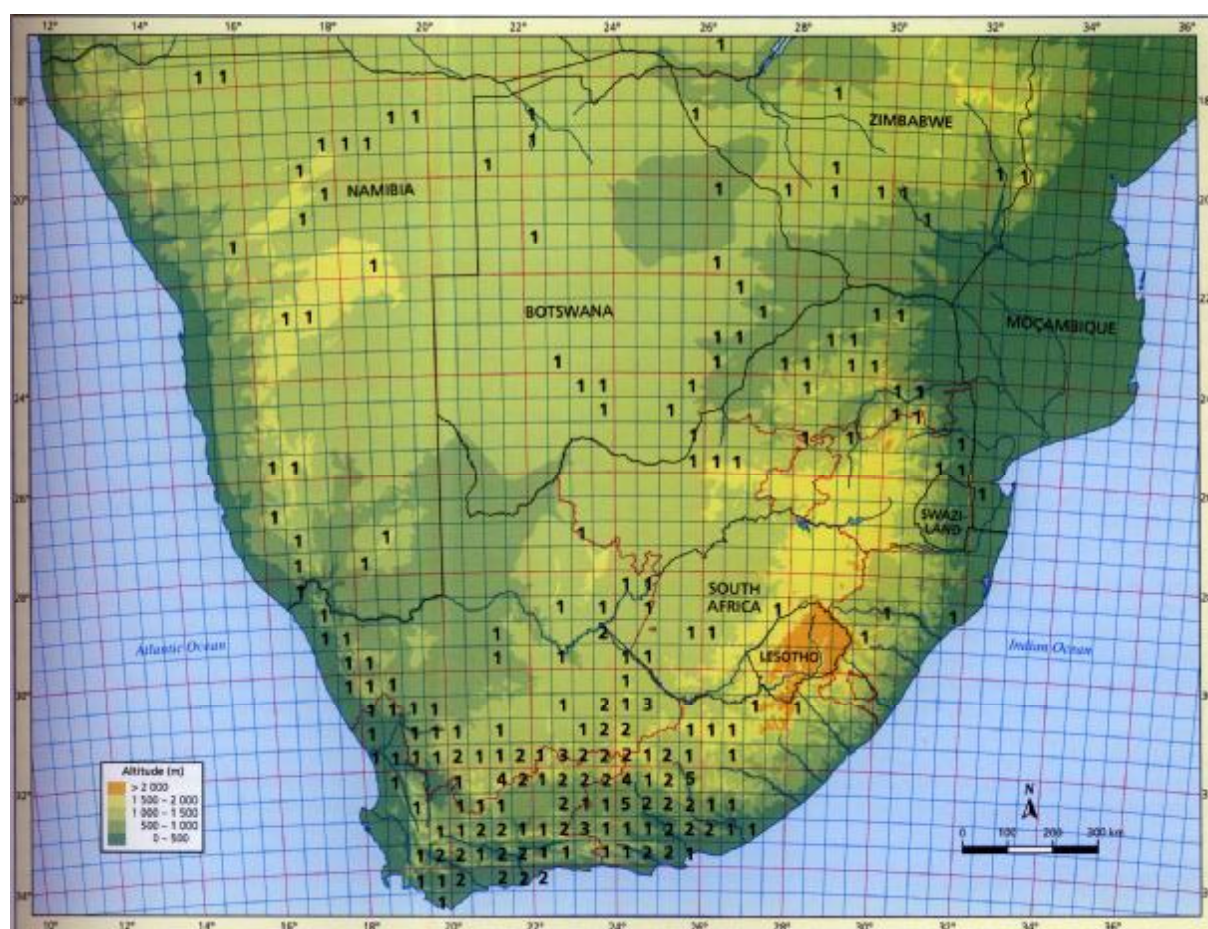


Fig. 3.2. Patterns of diversity in *Duvalia* in southern Africa, showing the number of species recorded to date in each half-degree square.

did Meve (1997) present any new evidence of this character. A more detailed examination of the inside of the respective guide-rails through the scanning electron microscope (fig. 34 A-C, G) shows that they are similar in both genera. Immediately behind the rail is a dense patch of papillae and behind this there is a smooth area which is raised into a ridge in both genera, though this ridge is somewhat more prominent in *Huernia* than in *Duvalia*. So actually in both genera the guide-rails are double.

The 'tubercle' at the mouth of the nectarial cavity is also problematic. Whereas in most species of *Huernia* it is quite obvious and situated just beneath the guide-rail so as to obscure the entrance to the nectarial cavity in *H. procumbens* it is particularly small. As it is situated well below the opening to the nectarial cavity, it cannot obscure the entrance at all. In *H. verekeri* it is absent. Consequently, while this character can be used to place most species in the correct genus, it cannot be used to discriminate between these genera.

Many of the apparently distinctive features of the flower in *Duvalia* can be matched in species of *Huernia* such as *H. procumbens*, *H. urceolata* and *H. verekeri*. This seems to suggest that, whereas most species are readily assigned to one of the genera, there are a few that are morphologically somewhat intermediate and that, consequently, the position is not quite as clear-cut as Leach (1969a, 1988) felt it to be. One character that separates the two genera reliably and does not seem to have been used until now is that in *Duvalia* the corolla tube is formed entirely by the annulus with the corolla more or less flat towards the centre, whereas in *Huernia* the centre of the flower always has a distinct depression and the annulus is only present as a thickening around the mouth of this depression. Molecular data show that *Huernia* (including *H. procumbens*) is very clearly defined but its relationships to *Duvalia* remain unresolved.

However, the same research has shown that *Duvalia* in the sense of Meve (1997) may

not be monophyletic. Meve & Liede (2002, fig. 4) found that the northern species *D. eilensis* was closest to *Ballyanthus prognathus*, while they considered that the two southern species belonged to a separate branch. Our data, in which five species of *Duvalia* were included, showed again that the northern species are closely allied to *B. prognathus* while the southern species form a separate lineage, in which *D. polita* is sister to the other species. However, the relationships between these lineages also remain unresolved.

Meve & Albers (1990a) subdivided the genus into sect. *Duvalia* (the southern taxa) and sect. *Arabica* (the north-eastern taxa), which could be separated as follows:

- Stems uniformly green to reddish, leaf-rudiments flattened above with small stipular denticles at base.....sect. *Duvalia*
 Stems greyish green, usually conspicuously mottled with red-brown, leaf-rudiments conical, stipular denticles absent.....sect. *Arabica*

DUVALIA

Meve (1997) recognised 17 species in all, of which 13 species made up his sect. *Duvalia*. In the present account only the species of sect. *Duvalia* are considered and these are reduced here from 13 to 10. The species were essentially delimited by Bayer (1977; 1984a) except for some confusion over the then rather little known *D. maculata* and little has been added since then except for the amplification of information on distribution. This is especially the case for *D. maculata*, whose distribution is now much better documented and has been shown to extend to the Free State. Its existence in Namibia has also been confirmed, with three collections having been made in that country during the period 1993-2000.

Duvalia Haw., *Syn. Pl. Succ.* 44 (1812).

Stapelia [unranked] *Duvaliae* Schult. in Roem. &

Schult., *Syst. Veg.* 6: 43 (1820).

Stapelia L. sect. *Duvalia* (Haw.) Decne. in DC, *Prodr.* 8: 661 (1844).

Lectotype: *Duvalia elegans* (Masson) Haw.

Dwarf spineless sometimes rhizomatous succulent forming mats 40-300 mm diam. Stems 8-100 mm long, 6-25 mm thick, decumbent, cylindrical or clavate to short and nearly spherical, fleshy and firm, glabrous, uniformly green to reddish or purplish; tubercles usually conical, spreading, fused near bases into 4-6 obtuse angles along stems with groove between them, narrowing into small not persistent deltoid-acute leaf-rudiment 1-4 (-6) mm long, flattened above and subtended by 2 glandular stipular denticles. Inflorescence glabrous, 1 per stem, arising mainly in

lower half of stem, bearing 1-8 (-20) flowers developing in gradual (rarely quick) succession from short peduncle (< 5 mm long), with lanceolate acute bracts < 2 mm long, sometimes with small lateral teeth; pedicel (3-) 8-25 (-40) mm long, 1-2.5 mm thick, spreading with ascending apex, holding flower facing upwards, usually close to ground; sepals 2-6 mm long, 1-2.5 mm broad at base, lanceolate, acuminate. Corolla 10-15 mm diam., rotate, deeply lobed; outside smooth and glabrous, without raised veins, with entral part flat, green to brownish; inside with central part massively thickened into fleshy circular to pentagonal annulus, papillate to hairy on annulus and around bases of lobes, uniformly pale yellow to nearly black, rarely mottled; tube 1-4 mm deep, shallowly conical to bowl-shaped, formed entirely by annulus; lobes 3.5-16 mm long, 1.5-8 mm broad at base, spreading, ovate-acute to narrowly ovate-acuminate but nearly always with margins deflexed and lobe longitudinally folded $\pm$ tightly along midrib so mostly slenderly linear-acute to -acuminate, often longitudinally somewhat rugulose, margins often ciliate. Corona 2.5-4.5 mm tall, 2-6 (-9) mm broad, consisting of 2 series arising on staminal tube and well separated from one another, glabrous, raised above base of tube on stipe 0.5-1.0 mm long; outer lobes forming pentagonal to circular spreading disc, included in tube to spreading on top of and covering annulus, without raised tubercle obscuring entrance to nectarial cavity; inner lobes 0.5-1.0 mm long, adpressed to backs of anthers and rarely slightly exceeding them, dorsiventrally flattened, obtuse, at base with rounded obtuse ascending to spreading dorsal projection 0.8-1.5 mm long. Anthers horizontal on top of style-head, margins shrinking back to expose pollinia, rectangular. Pollinium ellipsoidal, longer than

broad, insertion-crest exactly along outer edge, caudicle attached with broad cupular pad to base. Follicles erect, terete-fusiform, obclavate, slender, consisting of 2 horns diverging at 30-60°, longitudinally mottled with narrow broken purple stripes, glabrous, smooth.

In the southern African species of *Duvalia*, plants form clumps which vary from 40-300 mm in diameter. In a few species (some forms of *D. caespitosa*, in *D. immaculata* and *D. polita*) the stems are rhizomatous and in these the clumps can be fairly diffuse with scattered stems emerging from the soil over some distance. In other species the plants form mats, often with many small stems packed closely and tightly together. The stems are mostly short, cylindrical to clavate to almost spherical and, while never entirely prostrate, are usually close to the ground for most of their length, with a slightly upturned apex. They bear conical tubercles which are arranged in 4-6 rows along the stem. At the tip of each tubercle there is a narrowly triangular leaf-rudiment which is flattened above. This leaf-rudiment is very small in *D. parviflora* but may reach a maximum length of 6 mm in *D. polita*. In most cases these leaf-rudiments soon wither and fall off (often persisting as a small, weak spine in *D. polita*). There are invariably two small stipular denticles at the base of each leaf-rudiment.

Inflorescences are produced in the lower half of the younger stems and mostly only one arises on each stem. Flowers open in gradual

Key to the species

1. Annulus $\pm$ glabrous (papillae < 0.5 mm long) 2
2. Corolla inside cream, sometimes green to pale brown towards tips of lobes, 10-15 mm diam 10. *D. parviflora*
2. Corolla inside brown, red to purple (occasionally dull greenish), mostly > 15 mm diam 3
3. Outer corona enclosed within tube formed by annulus 4
4. Annulus pentagonal with undulating upper surface, narrowing towards base, corolla lobes tightly folded longitudinally 5
5. Annulus uniformly dark brown 8. *D. immaculata*
5. Annulus spotted with brown on cream 7. *D. maculata*
4. Annulus $\pm$ circular and not undulating above, becoming broader towards base, corolla lobes convex above but not folded longitudinally 6. *D. pillansii*
3. Outer corona $\pm$ level with or slightly above top of annulus 6
6. Corolla lobes tightly folded along midrib for whole length, annulus 3.0-4.5 mm diam., corona white 9. *D. angustiloba*
6. Corolla lobes folded along midrib in upper half but usually more laxly towards base, annulus > 5 mm diam. (rarely 4.5 mm diam.), corona brown to purple (rarely cream) 7
7. Annulus 1.0-1.5 mm tall 5. *D. modesta*
7. Annulus > 1.5 mm tall 8
8. Corolla lobes tightly folded longitudinally along midrib at least in upper half 3. *D. caespitosa*
8. Corolla lobes convex above and only laxly folded along midrib 1. *D. polita*
1. Annulus with conspicuous hair-like papillae > 1 mm long 9
9. Corolla with hair-like papillae over $\pm$ entire inner surface 10
10. Corolla lobes convex above and only laxly longitudinally folded, annulus indistinct and broadening towards base, outer coronal disc $\pm$ covering whole of annulus 4. *D. elegans*
10. Corolla lobes tightly longitudinally folded for at least half of length, annulus distinct and usually narrowing towards base, annulus not completely covered by outer coronal disc 3. *D. caespitosa*
9. Corolla with hair-like papillae limited to annulus and margins of lobes 11
11. Corolla (25-) 30-45 mm diam., annulus covered with hair-like papillae 2-4 mm long 2. *D. corderoyi*
11. Corolla 18-30 (-35) mm diam., annulus covered with hair-like papillae up to 1.5 (-2.2) mm long 3. *D. caespitosa*

succession (more rapidly in *D. angustiloba*). The pedicel is usually horizontal, often pressed to the ground, with an abruptly upturned apex so that the flower faces upwards.

Flowers in *Duvalia* are distinctive. Most of them are brown, occasionally speckled with yellow to cream towards the centre and rarely wholly cream (*D. parviflora*). The corolla is deeply divided and the more or less deltate, spreading lobes are longitudinally folded downwards along their midrib. In several species they are tightly folded so that each lobe forms a narrow blade; in others they are tightly folded towards the tips and more loosely towards the base (in all species the upper surface of the lobes is convex). In many of them the lobes are somewhat longitudinally ridged along the midrib towards the base. Below the lobes, the centre of the corolla is flat underneath but on the upper surface it is thickened by a circular to pentagonal, much swollen annulus which rises up around the base of the gynostegium and forms a small, shallowly bowl-shaped corolla tube (usually only 2-3 mm deep) right in the middle. In most species the coronal disc closes off the mouth of the tube so that it is visible only when the flower is dissected. In a few (*D. immaculata*, *D. maculata* and *D. pillansii*) this disc is lodged inside the tube and most of the tube is then visible. The inside of the tube is usually mottled with brownish on cream.

In all species of *Duvalia* the corona is raised up from the base of this tube on a column or stipe with a circular (not pentagonal) cross-section. This structure is of variable length, in some species raising the outer coronal disc right to the level of the mouth of the annulus, in others raising it only just above the base of the tube. The outer corona lobes are fused into a spreading, pentagonal to circular disc right around the gynostegium. Within this structure, beneath each guide-rail is a nectarial cavity which is fairly deep but laterally shallow and bounded on the outside by a lip formed by the outer corona (fig. 34 B). The inner corona lobes are well separated from the outer, with a small limb adpressed to the backs of the anthers and a broad, transverse, dorsal projection at their base, usually more massive than the lobes themselves.

The pollinaria in *Duvalia* are also distinctive (fig. 32 C is typical), with ellipsoidal pollinia each with a thick and quite short insertion-crest which lies exactly along the outer edge (but towards the apex of the Pollinium). The corpuscle is short and broad and has inordinately long lateral wings, which together are much longer than the breadth of the whole pollinarium. There is a broad, almost cup-like join of the caudicle to the base of the Pollinium.

Duvalia is found in both the southern and north-eastern parts of Africa. The species in the north-east, of which there are four making up

the sect. *Arabica*, are distributed along both sides of the Red Sea: in Arabia in south-western Saudi Arabia and south-western Yemen; and in Africa in Djibouti, Ethiopia, Somalia and the north-eastern extremities of the Sudan (Meve 1997).

Between these populations in north-eastern Africa and those of sect. *Duvalia* there is a remarkable gap of nearly 3000 km before the northernmost populations of *D. polita* are found in Zambia and Malawi. *Duvalia polita* is widely distributed in tropical and subtropical southern Africa. The remaining species are found much further south, in the arid and semi-arid parts of the former Cape Province, with outliers in southern Namibia and the Free State.

Most of southern Africa (fig. 3.2) has only one or fewer species of *Duvalia* per half degree square, usually provided by *D. polita* or *D. caespitosa*. A maximum of five is reached and, most unusually for the stapeliads, this happens in the Great Karoo, mainly near the southern edge of the escarpment and well outside the Succulent Karoo biome. A peak of four is achieved south-west of Fraserburg and four or five species are recorded in several squares between Aberdeen, Aberdeen Road and Cradock. Some of these species (such as *D. pillansii*) have been recorded extremely rarely so that, for example, the remarkable discoveries of Eustace Pillans around Aberdeen Road have never again been matched in the area. In addition, the peak of four around Fraserburg is almost entirely due to the interest in succulents by a local farmer (A.S. Theron), who has made several unexpected discoveries on his own and on neighbouring farms. It is therefore possible that these patches of higher concentration are not as disconnected as they appear at present and that future exploration will link them up.



Fig. 3.3. *D. polita*, 22 km north of Molepolole, Botswana, flowers with brightly mottled lobes, in habitat, December 1995.

1. *Duvalia polita*

Duvalia polita N.E.Br., Card. Chron. N.S. 6:130 (1876).

Type: South Africa, material widely cultivated in England (K).

Duvalia dentata N.E.Br., Bull. Misc. Inform. 1895: 265 (1895).

Type: Botswana, 30 miles north-west of Koobie, Baines (K).

Duvalia transvaalensis Schltr., Bot. Jahrb. Syst. 20, Beibl. 5: 54 (1895).

D. polita var. *transvaalensis* (Schltr.) A.C.White & B.Sloane, Stap., ed. 2, 2: 754 (1937).

Type: Transvaal, sandy places at Klipdam, Schlechter 4498 (BOL).

Duvalia transvaalensis var. *parviflora* L.Bol., Ann. Bot. Herb. 1: 194 (1915).

D. polita var. *parviflora* (L.Bol.) A.C.White & B.Sloane, Cact. Succ. J. (US) 14:159 (1942).

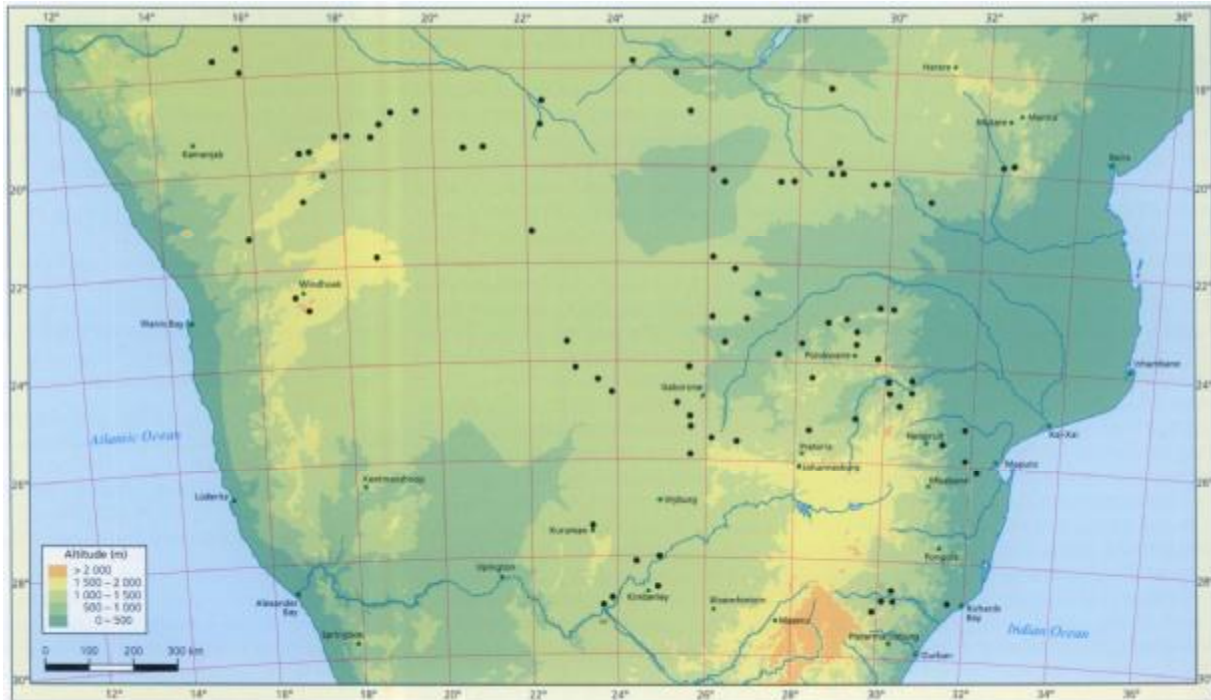
Type: Transvaal, Seringa, near Naboomspruit, Galpin 8467 (BOL).

Duvalia polita var. *polita* f. *intermedia* A.C.White & B.Sloane, Stap., ed. 2, 3:144 (1937).

Lectotype: White & Sloane, Stap., ed. 2, 2: fig. 751, upper flower.

Small succulent forming diffuse to dense clump to 150 mm diam., often spreading underground and forming new clumps. Stems 20-100 mm long, 7-15 mm thick (above ground), decumbent, often with slender runners spreading horizontally underground for up to 300 mm then rising up and becoming thicker and erect on emerging from soil, cylindrical, green to brown; tubercles 5-10 mm long, conical, arranged into 6 angles along stem, tapering gradually into lanceolate acuminate leaf-rudiment 4-6 mm long subtended by stipular denticles $\pm$ 0.5 mm long. Inflorescence arising near base of stem, of 1-4 flowers

DUVALIA POLITA



opening in gradual succession, with slender bracts up to 5 mm long; *pedicel* 15-25 mm long, 1 mm thick, spreading with ascending apex holding flower facing upwards; *sepals* 4-5 mm long, 1-2 mm broad at base. *Corolla* 20-35 mm diam.; outside pale green; inside shiny to dull reddish to dark purplish brown becoming paler around centre, sometimes spotted with these colours on yellow to cream background on lobes with darker purple-brown non-spotted centre; annulus 2.5-5.0 mm tall, 8-12 mm broad, circular, widening slightly towards base, covered with fine papillae < 0.5 mm long; *lobes* 10-15 mm long, 7-10 mm broad at base, ascending to spreading, convex above from lax longitudinal fold along midrib, ovate, acuminate, margins usually with vibratile purple clavate cilia 0.5-2.5 mm long for up to two thirds of length. *Corona* 4.5-6.5 mm diam., reddish brown; *outer lobes* forming circular to pentagonal disc at or just inside mouth of tube; *inner lobes* < 1 mm long, with obtuse ascending-spreading dorsal projection $\pm$ 1 mm long, somewhat paler than outer.

Distribution and habitat

Duvalia polita is the most widely distributed of all the 'southern Duvalias'. It is found extensively in the tropical parts of Namibia north of Windhoek, but well east of the Namib Desert. In Botswana it is also widely distributed, mainly around the edge of the country, although it is apparently rare in the sandy part north of the Okavango Delta and in the dry south-west. There are also several records from Zimbabwe,

all of them away from the wetter, central highlands. In South Africa it occurs in the Kimberley district in the former Transvaal and sporadically in KwaZulu-Natal (though it is very common in the driest parts of the Tugela River valley) and this is the only country where it occurs well outside the tropics, since it is recorded as far south as near Douglas, along the Orange River.

There are also a few records from the south of Angola (Kers 1969), where it has been collected a few times in the vicinity of Xangongo (Rocadas). Further records exist from Malawi, where it occurs in *Colophospermum mopane* woodland in the relatively low-lying valley of the Shire River south of Liwonde (Hargreaves 1979; own collection 1999), from Swaziland and



Fig. 3.5. *D. polita*, PVB 6483, Kangwa, Botswana, in habitat, December 1995.

from Zambia, where it may well be more widely distributed. It was also mentioned as growing in Mozambique (Gomes e Sousa 1936) and the only specimen that I have seen from there is a collection of L.C. Leach from near Goba at the foot of the Lebombo Mountains (LMA records).

Generally *D. polita* grows among trees or low bushes in sandy soil or on calcrete and it is quite often associated with *Colophospermum mopane* woodland.

Diagnostic features and relationships

Plants of *D. polita* form clumps up to 150 mm across but send out subterranean runners. These are slender and more or less terete and may spread horizontally beneath the surface for anything up to 300 mm, after which they rise up and, on emerging from the surface, become thicker and may remain solitary or form a new clump. Thus some larger plants can spread over an area of up to 1 sq m, consisting of many small clumps or, in some cases, just single, isolated stems scattered over this area.

The stems of *D. polita* are much longer relative to their thickness than in any of the other 'southern Duvalias'. When exposed, the above-ground parts may be quite short (only 20-40 mm tall), but if sheltered they may reach a height of 100 mm. They are somewhat cylindrical and six-angled, and when young they bear narrow, slender leaf-rudiments with quite obvious stipular denticles at their bases. At this stage they look quite spiky and rather like small stems of *Tavaresia*. The leaf-rudiments quickly dry out and soon wear off, leaving the stems looking very much like those of *Huernia longii*.



Fig. 3.6. *D. polita*, PVB 4138, north-east of Grootfontein, Namibia.

Flowers in *D. polita* are extremely variable in colour, frequently within individual populations. Some are bright, shiny and purple-brown on the lobes, with a slightly paler annulus which is very finely mottled with cream. The basic colour may also be a much paler reddish brown. In others the lobes are mottled with purple-brown on yellow to cream while the centre is uniformly purple-brown or red-brown, without mottling. As Meve (1997) indicated, there is no point in recognizing these different forms as separate taxa as they all occur together over much of the distribution of the species.

In *D. polita* the corolla lobes are not tightly folded along the midrib. Nevertheless, there is still a fold there, and the lobes are convex above but spread out almost fully beneath this fold so that the ovate and acuminate shape of each lobe is quite clear. Usually the lobes are adpressed to the ground near their bases and rise up towards their tips, mostly to a little above the height of the annulus. The annulus itself is comparatively large, usually widening slightly towards the base and has the outer coronal disc closing off the tube right at its mouth or slightly inside it. This disc is much smaller in diameter than the annulus itself but is only slightly broader than the full extent of the inner lobes.

History

Duvalia polita was described by N.E. Brown from plants that were quite widely cultivated in England at the time and were known to have come from somewhere in South Africa. Contemporary growers knew it as *Stapelia polita* or *S. echinata* but, until Brown published *D. polita*, it had been without a formal name.



Fig. 3.7. *D. polita*, PVB 2275, near Steinhausen, Namibia.

2. Duvalia corderoyi

Duvalia corderoyi (Hook. f.) N.E.Br., Bot. Mag.

102: sub t. 6245 (1876).

Stapelia corderoyi Hook. f., Bot. Mag. 100: t. 6082 (1874).

Type: South Africa, Aliwal North division, Burke (K).

Dwarf succulent forming mat 40-300 mm diam. Stems 12-45 mm long, 12-25 mm thick, decumbent, short and nearly spherical, dark green to reddish; tubercles 3-5 mm long, conical, arranged into 5-6 rows along stem, tapering gradually into deltoid acute leaf-rudiment 1.0-1.5 mm long subtended by 2 glandular stipular denticles. Inflorescence arising near base of stem, of 1-4 flowers developing in gradual succession, with small bracts 1-2 mm long; pedicel 15-25 mm long, 1.5-2.0 mm thick, ascending to hold flower facing upwards; sepals 4-5 mm long, 1.0-1.5 mm broad at base. Corolla (25-) 30-45 mm diam; outside brownish cream; inside yellow-brown, red-brown to dark purple or greenish, often shiny on lobes; annulus 2.5-4.0 mm tall, 9-15 mm broad, ± circular, vertically sided, mottled with brown on cream on upper part and into tube, covered with slender pale hair-like papillae 2-4 mm long; lobes 12-16 mm long, 3-5 mm broad at base, folded along midrib for whole length (tightly towards tips) so narrowly lanceolate-acuminate, longitudinally faintly rugulose, glabrous except for purplish viridate clavate cilia 2-4 mm long along margins for two thirds of length changing to short cylindrical hairs near base and in sinuses of lobes and towards tips. Corona 6-9 mm diam; outer lobes forming circular to pentagonal disc spreading at or just inside mouth of tube, pinkish red to red-brown or purple; inner lobes 1 mm long, with ascending obtuse dorsal projection ± 15 mm long, cream to reddish brown.

Distribution and habitat

Duvalia corderoyi is reasonably widespread over much of the Great Karoo above the escarpment at between 1000 and 1600 m but keeping well south of the drier, north-western parts (such as Bushmanland) and north of the dry and relatively low-lying south-east (Port Elizabeth to Jansenville). It is found from south-west of Fraserburg to Beaufort West and Victoria West and eastwards to Graaff-Reinet and Cradock, continuing north-eastwards to Colesberg and around Bloemfontein and Ficksburg in the Free State.

Plants of *D. corderoyi* are always found under small bushes on stony ground, usually in flatfish spots and frequently amongst scattered dolerite rocks.

Diagnostic features and relationships

In *D. corderoyi* the plant may form a mat up to 300 mm across, with very large numbers of stems tightly packed into such a clump and sometimes even forming several layers packed on top of one another. The stems are thicker than in most of the other species but

DUVALIA CORDEROYI

always remain short and are nearly spherical in outline. They have also rather more robust conical tubercles arranged weakly into six rows along the stems and these six-angled stems distinguish it easily from most of the species with which it occurs (except occasionally from robust forms of *D. caespitosa*). Older stems, where the leaf-rudiments have worn off, can begin to resemble those of *Pectinaria articulata*.

Flowers in *D. corderoyi* are larger than in any other of the southern African species and are generally at least 30 mm across. The basic colour of the corolla lobes is usually brown, but may be yellowish, reddish or purplish on occasion. The lobes are not very tightly folded and, in the lower half, are usually only reflexed. They are lined with dark, vibratile cilia. The fairly tall and conspicuous annulus is usually attractively and fairly clearly mottled on the upper surface with brownish on a cream background. There is always a dense beard of pale, white to purplish hairs on the annulus and down its sides between the lobes and these give a soft, cushion-like appearance to the centre. As mentioned by Meve (1997), the hairiness combined with the size of the flower is most suggestive of the north-eastern species *D. sulcata*, though it is more closely related to the southern species than to any of the north-eastern ones.

History

Duvalia corderoyi was first collected by Joseph Burke, who brought live specimens back to London from his joint expedition with Carl Zeyher. It appears that these specimens were found near the Orange River in the Aliwal North district and it is likely that they were collected on the return journey near Colesburg

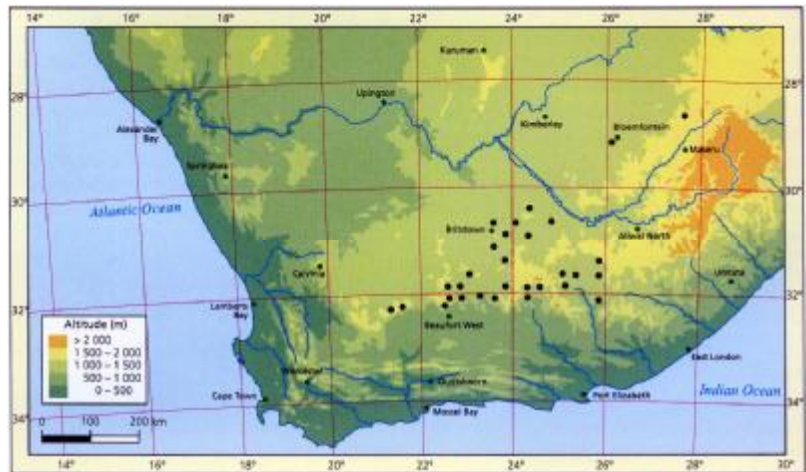


Fig. 3.8. Distribution of *Duvalia corderoyi*.

in February 1842. Hooker published the name only in 1874, naming the species after Justus Corderoy, a well-known cultivator of succulents who lived at Blewberry near Didcot in England. The plants seem to have survived for a long time in cultivation, as Hooker mentioned that it flowered in Corderoy's care in September 1873 and N.E. Brown (1890) mentioned growing a piece from the same plant.

N.E. Brown was particularly partial to this species and considered it to be the 'finest species' of *Duvalia* that was known to him. He also noted (Brown 1890), though, that the figure published by Hooker and painted by the usually very reliable W. Fitch had unnaturally bright colours and badly drawn buds, so that this figure did not give an accurate impression of it.



Fig. 3.9. *D. corderoyi*, PVB 5972, east of Fraserburg, an unusual, yellowish variant, in habitat, April 1994.

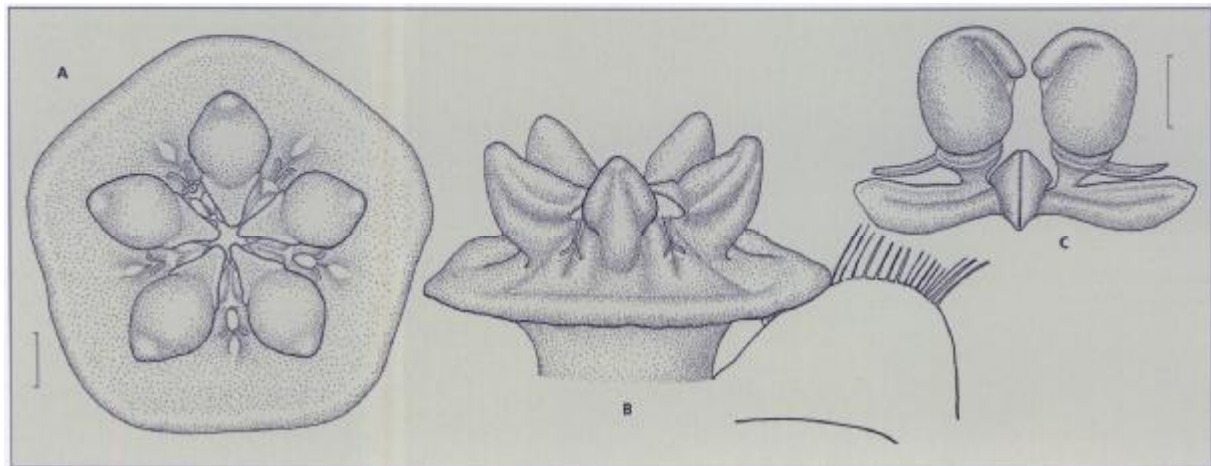


Fig. 3.10. *Duvalia corderoyi*. A, face view of gynostegium. B, side view of centre of dissected flower. C, pollinarium (outgrowths on the side of the caudicles are not always present). Scale bars: A, B, 1 mm (at A); C, 0.25 mm. Drawn from: A, B, PVB 4223, Deelfontein; C, PVB 3073, near De Aar.



Fig. 3.11. *D. corderoyi*, PVB 5972, south-west of Fraserburg.



Fig. 3.12. *D. corderoyi*, PVB 5972, east of Fraserburg, with somewhat pinkish flowers, in habitat, April 1994.



Fig. 3.13. *D. corderoyi*, PVB 6275, south-west of Fraserburg.



Fig. 3.14. *D. corderoyi*, PVB 4223, Deelfontein siding. Here the flower has especially long hairs on the annulus.

DUVALIA CAESPITOSA

3. *Duvalia caespitosa*

Duvalia caespitosa (Masson) Haw., Syn. Pl. Succ: 45 (1812).

Stapelia caespitosa Masson, Stap. Nov.: 20, t. 29 (1797).

Type: South Africa, Cape, Masson (missing).

Lectotype: Masson, Stap. Nov.: t. 29.

Dwarf succulent forming mat 60-300 mm diam. Stems 10-100 (-150) mm long, (4-) 6-22 mm thick, decumbent and occasionally rhizomatous, green to reddish green; tubercles 3-5 mm long, conical, fused near bases into 4-5 (-6) broadly obtuse rows along stem with groove between them, abruptly narrowing into narrowly deltoid leaf-rudiment 1.5-2.0 mm long subtended by small stipular glands. Inflorescences 1 (-3) per stem arising mainly in lower half, each of 1-3 flowers opening in gradual succession, with few small lanceolate bracts 1-3 mm long; pedicel 10-25 mm long, 1.5-2.5 mm thick, spreading with ascending apex, holding flower facing upwards close to ground, purplish green; sepals 3-6 mm long, 1.0-2.5 mm broad at base. Corolla 18-30 (-35) mm diam.; outside pale brownish green; inside pinkish red to chocolate to dark purple or nearly black, often shiny on lobes; annulus (1.0-) 2-5 mm tall, 6-12 mm broad, circular to pentagonal,

vertically sided, with white to yellow spots on top and in tube, often covered with hair-like papillae 0.4-1.5 (-2.2) mm long; tube 1.5-3.0 mm deep; lobes 9-15 mm long, 3-5 (-9) mm broad at base, folded tightly along midrib for at least half of length and there narrowly linear-acute, sometimes with clavate vibratile cilia up to 2.5 mm long along margins in lower half. Corona 3-5 mm tall, 4.5-7.0 mm broad; outer lobes forming circular to pentagonal disc spreading at or just inside mouth of tube, reddish brown, orange- to purple-brown; inner lobes 0.5-1.5 mm long, with ascending obtuse dorsal projections 1.0-1.5 mm long, yellow to brownish purple.

Duvalia caespitosa is the most widespread species of *Duvalia* outside the tropics (i.e. other than *D. polita*). The distribution begins around Aus in south-western Namibia and collections have been made over most of Namaqualand as far south as Clanwilliam, on the Worcester-Robertson Karoo and Little Karoo as well as onto the coastal plain around Swellendam, Bredasdorp and Mossel Bay. It is also widespread, though somewhat less common, on the Great Karoo as far east as the Free State and the northern parts of the Eastern Cape near Maclear.

Key to the subspecies of *D. caespitosa*

1. Corolla inside noticeably pubescent 2
2. Plants from Namaqualand, not at all rhizomatous, corolla often somewhat pinkish inside 3b. subsp. *pubescens*
2. Plants from south of Langeberg (southern Cape), often somewhat rhizomatous, corolla red-brown to nearly black 3c. subsp. *vestita*
1. Corolla inside very slightly pubescent to nearly glabrous 3a. subsp. *caespitosa*

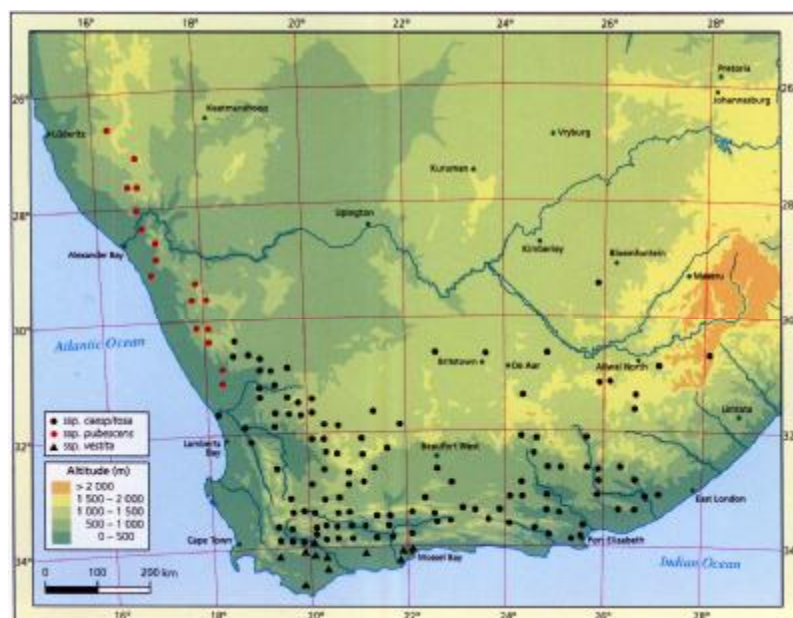


Fig. 3.15. Distribution of *Duvalia caespitosa*.

3a. *Duvalia caespitosa* subsp. *caespitosa*

Stapelia reclinata Masson, Stap. Nov.: 19, t. 28 (1797).
Duvalia reclinata (Masson) Haw., Syn. Pl. Succ: 44 (1812).

Type: South Africa, Cape, Masson (missing).

Lectotype: Masson, Stap. Nov.: t. 28.

Stapelia radiata Sims, Bot. Mag. 17: t. 619 (1803).

Duvalia radiata (Sims) Haw., Syn. Pl. Succ: 45 (1812).

Lectotype: Bot. Mag.: t. 619.

Stapelia hirtella Jacq., Stap.: t. 10 (1806-19).

Duvalia hirtella (Jacq.) Sweet, Hort. Brit., ed. 1: 276 (1826).

Stapelia caespitosa var. *hirtella* (Jacq.) Loud., Encycl. Pl.: 202 (1841).

Duvalia radiata var. *hirtella* (Jacq.) A.C. White &

B. Sloane, Stap., ed. 2: 779 (1937).

Lectotype: Jacq., Stap.: t. 10.

Stapelia replicata Jacq., Stap.: t. 15 (1806-19).

Duvalia replicata (Jacq.) Sweet, Hort. Brit., ed. 1: 276 (1826).

Lectotype: Jacq., Stap.: t. 15.

Duvalia compacta Haw., Syn. Pl. Succ: 46 (1812).

Stapelia compacta (Haw.) Schult., in Roem. & Schult.,

Syst. Veg. 6: 46 (1820).

D. caespitosa var. *compacta* (Haw.) Meve, *Duvalia*:

59 (1997).

Type: *Duvalia compacta* (OXF).

Stapelia mastodes Jacq., Stap.: t. 13 (1806-19).

Duvalia mastodes (Jacq.) Sweet, Hort. Brit., ed. 1:

276 (1826).

Lectotype: Jacq., Stap.: t. 13.

Duvalia propinqua A. Berger, Monatsschr. Kakt.: 24

(1904).

Type: cultivated specimen, La Mortola (NY, holo;

K, iso).

Duvalia hirtella var. *minor* N.E. Br., Fl. Cap. 4 (1): 1031

(1909).

D. radiata var. *minor* (N.E. Br.) A.C. White & B. Sloane,

Stap., ed. 2: 781 (1937).

Type: Worcester distr., N.S. Pillans 628 (missing).

Duvalia hirtella var. *obscura* N.E. Br., Fl. Cap. 4 (1):

1031 (1909).

D. radiata var. *obscura* (N.E. Br.) A.C. White &

B. Sloane, Stap., ed. 2: 778 (1937).

Lectotype: near Matjiesfontein, N.S. Pillans 13 (K).

Duvalia reclinata var. *angulata* N.E. Br., Fl. Cap. 4 (1):

1030 (1909).

Type: Ladismith, N.S. Pillans 615 (missing).

Duvalia reclinata var. *bifida* N.E. Br., Fl. Cap. 4 (1):

1030 (1909).

Type: Glen Avon Estate, N.S. Pillans 27 (K, holo;

BOL, iso).

Duvalia emiliana A.C. White & B. Sloane, Stap., ed. 1:

126 (1933).

Type: White & Sloane 143 (missing).

Lectotype: White & Sloane, Stap., ed. 2: 760.



Fig. 3.16. *D. caespitosa* subsp. *caespitosa*, PVB 6047, south-west of Calvinia.



Fig. 3.17. *D. caespitosa* subsp. *caespitosa*, PVB 7532, Stuurmans, east of Calvinia, here with very pale annulus. This and the next two pictures give some idea of the variability of this taxon in a single locality.



Fig. 3.18. *D. caespitosa* subsp. *caespitosa*, PVB 7532, Stuurmans, east of Calvinia.



Fig. 3.19. *D. caespitosa* subsp. *caespitosa*, PVB 7532, Stuurmans, east of Calvinia, in this case with deeply mottled annulus.

Stems 10-100 (-150) mm long, 6-22 mm thick, rarely somewhat rhizomatous. Corolla 16-35 mm diam.; inside red-brown to nearly black, with hair-like papillae 0.2-1.0 mm long variably present mainly on annulus; annulus 1.2-5.0 mm tall, 5.5-11 mm broad; lobes with margins sometimes ciliate.

Distribution and habitat

Subsp. *caespitosa* is found in most suitably dry habitats in the Western, Northern and Eastern Cape from southern Namaqualand to the Worcester-Robertson Karoo, the Ceres Karoo, Little Karoo and the Great Karoo as far east as Graaff-Reinet, Fort Beaufort and Grahamstown. Further east of this it becomes scarce, with only a few localities known in the Free State and the northern parts of the Eastern Cape.

Over this vast area it is found in a wide variety of habitats but mostly it prefers stony places under small bushes, frequently with a wide selection of other succulents. Plants are often found together with species of *Piранthus* and they frequently grow under shrublets of *Ruschia spinosa*.

Diagnostic features and relationships

Vegetatively subsp. *caespitosa* is remarkably variable. Plants with thick, five-angled stems sometimes up to 60 mm long, are often found growing together with others with very small, four-angled stems no more than 20-30 mm long. Most specimens grow only on the surface but in several areas, notably from Humansdorp to Hankey, the stems can be slender, somewhat cylindrical and less clearly five-angled and distinctly rhizomatous (fig. 10). In such instances they are difficult to distinguish from plants of *D. immaculata*.

In a typical flower the corolla lobes are strongly folded for their whole length along the midrib to form narrow, spreading, shiny to quite dull, vertical blades radiating from the centre. Mostly they are chocolate-brown but they may be reddish, faintly yellow or even nearly black. The central part is raised into an often quite steeply cylindrical annulus (in other cases rather low and flattened), covered on the top and into the tube with hair-like papillae which sometimes extend onto the outside of the annulus and even out onto the lobes. Variability in certain populations in the length of these papillae and the extent to which they cover the corolla can be remarkably wide. This has been observed especially on the Worcester-Robertson Karoo, where it can be very plentiful. On the outside the annulus is usually also chocolate-coloured but just inside the mouth of the tube it becomes pale yellow, finely speckled with brown and this colour continues down into the base of the tube under the outer corollal disc. Often in a population, there will be a

few plants where the rim of the annulus is also yellowish or mottled with brown on white. The outer corollal disc is mostly dull reddish brown (sometimes even yellow), usually only slightly pentagonal and mostly smaller than the diameter of the annulus but more or less enclosing all of the corolla-tube.

History

This is another of the many plants discovered by Francis Masson and he collected material of it at an undisclosed location on the Karoo in the Cape.



Fig. 3.20. *D. caespitosa* subsp. *caespitosa*, PVB 6894, east of Adelaide in the Eastern Cape.



Fig. 3.21. *D. caespitosa* subsp. *caespitosa*, PVB 5047, near Molteno in the Eastern Cape.



Fig. 3.22. *D. caespitosa* subsp. *caespitosa*, south-east of Worcester and indistinguishable from some of the flowers in subsp. *pubescens*, flowering in habitat, April 2001.

3b. *Duvalia caespitosa* subsp. *pubescens*

Duvalia caespitosa subsp. *pubescens* (N.E.Br.)
Bruyns, comb. et star. nov.
Duvalia pubescens N.E.Br., Fl. Cap. 4 (1): 1029 (1909).
Type: South Africa, plant cultivated at Cambridge,
England in 1881 (K).
Duvalia elegans var. *namaquana* N.E.Br., Fl. Cap. 4
(1): 1028 (1909).
Type: Little Namaqualand, Barkly 34 (K).
Duvalia pubescens var. *major* N.E.Br., Fl. Cap. 4 (1):
1029 (1909).
Type: Little Namaqualand, Scully (K).

Stems 10-50 mm long, 6-22 mm thick, not at all
rhizomatous. Corolla 18-32 mm diam.; inside pink-
brown to purplish, covered at least on annulus and bases
of lobes with hair-like papillae 0.5-1.5 mm long; annulus
1.5-3.0 mm tall, 6-12 mm broad; lobes with margins
not at all ciliate.

Distribution and habitat

Subsp. *pubescens* is found in Namibia from Aus
southwards to Rosh Pinah, mainly in the higher
mountains just east of the coastal plain. It con-
tinues southwards into the Northern Cape,
from Helskloof and Cornellsberg southwards
to around Springbok and to Kamieskroon and
Studer's Pass near Garies. Mostly it is found
at higher altitudes (600-1 200 m) in the gneiss
mountains of the Kamiesberg, but exceptions
can easily be found, as on quartzites of the
Augrabies Mountain at an altitude of about
400 m and within 25 km of the sea. It is mainly
found in localities where most of the rainfall is
received in winter.

Diagnostic features and relationships

Plants of subsp. *pubescens* are usually small,
with many densely packed, often very small
stems which, especially in Namibia and the
Richtersveld, are frequently not much more
than 15 mm long and even less in diameter.
However, they are quite variable and the stems



Fig. 3.23. *D. caespitosa* subsp. *pubescens*, PVB 6114,
north-east of Kamieskroon, in this case indistinguishable
from subsp. *vestita*.



Fig. 3.24. *D. caespitosa* subsp. *pubescens*, PVB 6114,
north-east of Kamieskroon.

are not uncommonly 30-40 mm or longer on
plants in the Kamiesberg, especially if they are
sheltered.

The flowers of subsp. *pubescens* are often
fairly pale, dull pink-brown rather than the
usual chocolate, especially in the northern areas
(Namibia and Richtersveld) but towards the
south they become darker and more shiny. The
annulus shows the same variation in colour as
that found in subsp. *caespitosa*, from yellowish
to speckled with brown to dark brown. The
lobes are usually tightly folded but, in a few
cases, have been found with broader, deltate
bases. This taxon is particularly characterized
by the pubescence of the corolla which is
covered, at least in the centre and often over
the whole surface, with fine hairs.

Meve (1997) mentioned that it differs from
subsp. *caespitosa* by its 'pubescent corolla sur-
face'. However, this is present in subsp. *caes-
pitosa* too (as one may see clearly in his figures
21 and 22). As the hairs may also become quite
sparse in some plants of 'pubescens' from the
Kamiesberg, this does not always provide a
reliable means of separating them. The dif-
ferentia between these two taxa are therefore
very weak and the differences between 'typical
caespitosa' and 'typical *pubescens*' are actually
smaller than the variation that will be found
within some more prolific populations of subsp.
caespitosa, for example, in the Worcester-Rob-
ertson Karoo. Bayer (1984a) and Spearing (1998)
have cast doubt on the distinctness of this taxon

as a species and it is here placed once more
under *D. caespitosa* since its allopathic distri-
bution with subsp. *caespitosa* suggests that
it is merely a northern form of *D. caespitosa*.
They differ principally in that in 'pubescens' the
corolla usually has hairs over most of the inner
surface while in 'caespitosa' hairs, if present,
are mainly found on the annulus and around
the base of the lobes.

History

Duvalia pubescens was described from material
of unknown origin which was in cultivation at
Cambridge in 1881 (Brown 1907-09). N.E.
Brown published the name and description
only in 1909, by which time he had also come to
see material that had been collected by Charles
Ayres (see under *Quaqua inversa*) and sent on
to him by N.S. Pillans.



Fig. 3.25. *D. caespitosa* subsp. *pubescens*, PVB 5357,
north-east of Kamieskroon. The flowers in this and the
next picture, apart from increased pubescence, are
indistinguishable from those of subsp. *caespitosa*.



Fig. 3.26. *D. caespitosa* subsp. *pubescens*, PVB 5357,
north-east of Kamieskroon.



Fig. 3.27. *D. caespitosa* subsp. *pubescens*, PVB 3930,
east of Rosh Pinah, Namibia, with the slightly pinkish
colouring and small flowers often seen in northern
Namaqualand and southern Namibia.

3c. *Duvalia caespitosa* subsp. *vestita*

Duvalia caespitosa subsp. *vestita* (Meve)
Bruyns, comb. et stat. nov.

Duvalia vestita Meve, *Kakt. and Sukk.* 39:197 (1988).
Type: South Africa, 2 km north of Wiedersdrift, Meve & Liede 397 (K, holo.; MSUN, iso.).

Stems 10-70 (-100) mm long, (4-) 6-22 mm thick, often somewhat rhizomatous. Corolla 20-30 mm diam.; inside red-brown to nearly black, covered at least on annulus and bases of lobes with hair-like papillae 0.5-2.2 mm long; annulus (1-)1.5-3.0 mm tall, 7-10 mm broad; lobes with margins not ciliate.

Distribution and habitat

Subsp. *vestita* is found south of the Langeberg on the coastal plain from near Greyton (north of Caledon) in the west to near Struisbaai in the extreme south and then very sporadically to around Mossel Bay. Meve (1997) listed two collections from the Worcester-Robertson Karoo but collections made subsequently at one of these has merely turned up subsp. *caespitosa* with a somewhat more-than-usually hairy annulus. These are therefore included now under subsp. *caespitosa*. Also listed was a collection from the Baviaanskloof but this is considered very unlikely and is omitted from the map.

Plants are found in gravelly flattish areas or low ridges, sometimes on shales and sometimes on limestones. It usually grows with other succulents (often including *Orbea variegata*) in locally arid spots covered with a very sparse, low vegetation.

Diagnostic features and relationships

Meve (1997: 106) mentioned the 'often elongated stems with rhizomatous tendencies' as diagnostic but in Meve (1988b) the fact that, in material other than the type, the stems could be considerably shorter and exhibited less of a tendency to produce rhizomes was discussed. In material from the arid, limestone areas south and south-east of Bredasdorp plants conform to the type quite closely in having slender, cylindrical, often elongated stems with a distinctly rhizomatous habit. However, in plants found on shales (e.g. at Stormsvlei and Napky), where they grow on stony hillsides or in flats, the stems are much thicker and ellipsoidal, with conspicuous tubercles and angles and in these situations they do not develop rhizomes at all (fig. 9). In this context it is worth noting the existence of cylindrical stems and a rhizomatous habit in some plants of subsp. *caespitosa* from around Hankey (fig. 10, in which the flower is wholly glabrous). It seems therefore that the shape of the stems and the rhizomatous habit are simply two more of the variable features of this exceedingly variable species.

In the key (Meve 1997:47), *D. pubescens* and *D. vestita* were separated as follows.

12. Corolla ad axially pubescent (sometimes missing on apices of corolla lobes), hairs whitish, at least 1 mm long, basal epidermis dull; corolla lobes $\pm$ completely replicate = *pubescens*

- Corolla pilose, hairs purplish > 1 mm long, basal epidermis brilliant, corolla lobes not or incompletely replicate = *vestita* (and *D. elegans*).

However, in the description (p. 99) of *D. pubescens*, the hairs are given as 'sometimes only on the basal half [of lobes], hairs 0.5-1.4 mm long'. For *D. vestita* (p. 102) the corolla lobes are 'ad axially pubescent to pilose on basal half to whole lamina...hairs up to 2.2 mm long'. This does not correspond to what is in the key and so there does not appear to be any difference here on which one might be able to separate the two species.

As far as the extent of folding of the corolla lobes is concerned, for *D. vestita* this is given as 'widely replicate' and for *D. pubescens* also as 'widely replicate' in the respective descriptions. In my experience of *D. vestita*, the corolla lobes are sometimes tightly replicate for almost their whole length (as is the case in Meve's Plate 3B) and they vary from this to hardly replicate at all. Much the same variation is present in *D. pubescens* so it does not seem that this can be used to separate them.

Meve mentioned that *D. vestita* had been 'confused with *D. pubescens*'. However, it seems that one could be forgiven for some confusion since, even with the best will in the world, I have problems seeing the differences between his Plate 3A (*pubescens*) and Plate 3B (*vestita*). Certainly the hairs on the corolla are similarly distributed in both and they are not visibly more whitish in '*pubescens*' than in the other. The only difference I have been able to notice is that the former is brownish and the latter more blackish with slightly shorter lobes. The two species seem to be impossible to separate with any reliability from each other and from *D. caespitosa* and both are here included as geographic variants under *D. caespitosa*.

In the Worcester-Robertson Karoo and around Montagu, *D. caespitosa* is common in some places and a wide range from glabrous to pubescent flowers is found. In a few cases specimens with pubescent annuli and corollas have been pressed and these have been determined by Meve (though not always cited) as '*Duvalia vestita*' (e.g. Olifantsdoorn, Bayer 680; Karoo Garden, Hall; Ashton, Bayer sub KG 299/71, all at NBG). However, there is so much variation in these populations that it would be more accurate to view these as pubescent-flowered individuals from among a range of variants which have been observed in subsp. *caespitosa* in this area. Further south it would appear that the glabrous-flowered forms disappear



Fig. 3.28. *D. caespitosa* subsp. *vestita*, PVB 6655, De Hoop, east of Bredasdorp. A plant with flowers very similar in shape to those often seen in subsp. *pubescens*.



Fig. 3.29. *D. caespitosa* subsp. *vestita*, PVB 6697, Wiedersdrift, south of Bredasdorp.



Fig. 3.30. *D. caespitosa* subsp. *vestita*, PVB 6697, Wiedersdrift, south of Bredasdorp.

entirely, leaving only the pubescent-flowered ones which constitute the subsp. *vestita*.

The relationship of this taxon to *D. elegans* around Riversdale is not clear. Plants of *Duvalia* have been found in several localities from Heidelberg to east of Riversdale and all of them have turned out to have the brightly shiny flowers of *D. elegans*. It appears that *D. caespitosa* does not occur in this area, although there are a few specimens which have been determined, apparently incorrectly, as *D. caespitosa*.

History

Subsp. *vestita* seems to have been observed for the first time by M. Bruce Bayer between Caledon and Riviersonderend in 1971. The material that was collected on the coastal flats south of Bredasdorp and described as *Duvalia vestita* was gathered in November 1986 but was first observed in this area by Bayer in 1980. Meve (1997) also cited some plants collected by Muir in 1951 at Riversdale but it is doubtful whether these really are '*vestita*' as they seem to belong to *D. elegans*.

DUVALIA ELEGANS

4. *Duvalia elegans*

Duvalia elegans (Masson) Haw., Syn. PL Succ: 44 (1812).

Stapelia elegans Masson, Stap. Nov.: 19, t. 27 (1797).
Type: South Africa, Cape, Karroo, Masson (missing).

Lectotype: Masson, Stap. Nov.: t. 27.

Stapelia radiata Jacq., Stap.: t.12 (1806-19), nom. illegit., non Sims (1803).

Lectotype: Jacq., Stap.: t.12.

Duvalia jacquiniana (Schult.) Sweet, Hort. Brit., ed. 1: 276 (1826).

Stapelia jacquiniana Schult. in Roem. & Schult., Syst. Veg. 6: 45 (1820).

Lectotype: Jacq., Stap.: t.12.

Duvalia elegans var. *seminuda* N.E.Br., Fl. Cap. 4 (1): 1028 (1909).

Type: Cape, 0.5 miles west of Riversdale, Nov. 1904, N.S. Pillans 682 (BOL).

Duvalia elegans var. *elegans* f. *magnicorona* A.C.White & B.Sloane, Stap., ed. 2, 3:1144 (1937).

Lectotype: White & Sloane, Stap., ed. 2, 2: fig. 729.

Dwarf succulent forming mat 40-80 mm diam. Stems 15-60 mm long, 4-12 (-18) mm thick, decumbent, short and nearly spherical to slender and cylindrical, green to reddish; *tubercles* 1-4 mm long, conical, arranged into 4-5 rows along stem, tapering abruptly into deltoid acute leaf-rudiment 1.0-1.5 mm long subtended by 2 stipular glands. Inflorescence arising mostly near base of stem, with small deltoid bracts < 1 mm long; *pedicel* 12-25 mm long, 1 mm thick, spreading with ascending apex holding flower facing upwards (often on ground); *sepals* 2.0-3.5 mm long, 1 mm broad at base. *Corolla* 13-22 mm diam.; outside brownish green; inside shiny dark purple-brown

becoming pale green speckled with maroon in tube, covered with slender dark purple hair-like papillae 1-3 mm long (except sometimes at apices of lobes); annulus 0.8-1.5 mm tall, 6-8 mm broad, indistinct, $\pm$ circular with sides spreading outwards towards bases of lobes; *tube* $\pm$ 1 mm deep; *lobes* 4.0-10.0 mm long, 2.5-6.0 mm broad at base, longitudinally laxly folded along midrib and only narrow near apex, rest convex above. *Corona* 5-7 mm diam.; *outer lobes* forming circular to pentagonal disc, sometimes with 5 distinct broad lobes each with apical notch, spreading at mouth of tube and $\pm$ covering annulus, pale brown to reddish brown to dark purple; *inner lobes* $\pm$ 0.5 mm long, with ascending to spreading obtuse dorsal projection $\pm$ 1 mm long, reddish cream.

Distribution and habitat

Duvalia elegans is restricted to the south-western Cape at altitudes of between 150 and 400 m from just west of Robertson in the Worcester-Robertson Karoo eastwards to Montagu and southwards to Drew and near Stormsvlei. It is also known from some of the small patches of natural *renosterveld* at Heidelberg and around Riversdale which have survived the agricultural 'holocaust' of the Swartland. The 'record' of this species from Namibia is considered highly doubtful, as suggested by Meve (1997).

Plants of *D. elegans* are generally found under small bushes, on stony to gravelly ground with a wide selection of other succulents typical of these areas. South of the Langeberg it is often associated with *Euphorbia tridentata* and various species of *Haworthia*. In the Worcester-Robertson Karoo it is frequently sympatric with *D. caespitosa*.

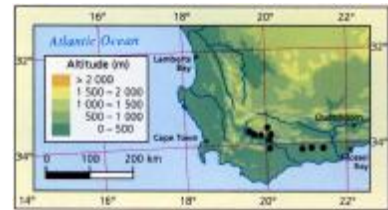


Fig. 3.31. Distribution of *Duvalia elegans*.

Diagnostic features and relationships

Specimens of *D. elegans* are usually small and form fairly diffuse clumps. The plants may consist of short, nearly spherical stems but may also have much longer, cylindrical stems where the tubercles are longer, fewer and very indistinct. Such cylindrical stems frequently tend to spread for some distance beneath the surface of the soil and then they assume the rhizomatous habit that is commonly found in *D. immaculata*.

Flowers of *D. elegans* are mostly less than 20 mm across and so are relatively small. The visible part of the corolla is darkly coloured and shiny, usually a deep purple-brown, but this changes to pale green speckled with maroon in the tube hidden under the corona. The margins of the lobes are reflexed and are not tightly folded downwards (except in some plants from between Heidelberg and Riversdale), so that the lobes generally have a narrowly deltate shape. Most of the corolla is fairly densely covered inside with conspicuous, dark purple hairs, though in some cases this thins out near the

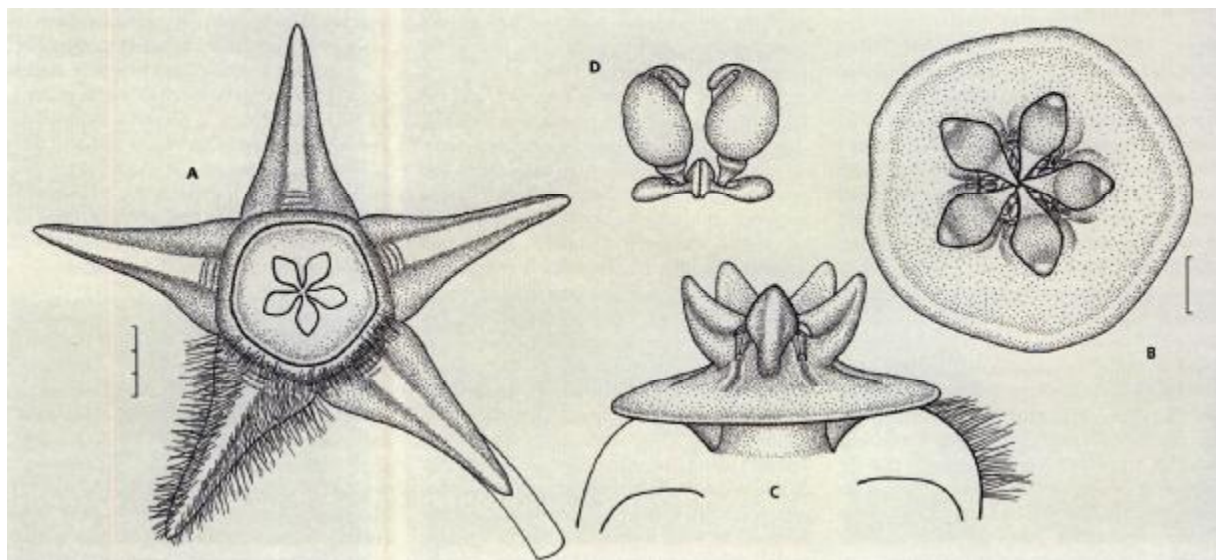


Fig. 3.32. *Duvalia elegans*. A, face view of flower. B, face view of gynostegium. C, side view of centre of dissected flower. D, pollinarium. Scale bars: A, 3 mm; B, C, 1 mm (at B); D, 0.25 mm (at A). Drawn from: PVB, west of Robertson.



Fig. 3.33. *D. elegans*, PVB 6703, near Drew, on the Worcester-Robertson Karoo.



Fig. 3.34. *D. elegans*, PVB 7643, east of Riversdale, on the coastal plain.

tips of the lobes. The annulus in the centre is partly obscured by the denseness of these hairs but it is also fairly indistinct and low, usually widening towards the base into the lobes. It is also made more inconspicuous by being hidden almost completely by the outer coronal disc. This disc is often dark-coloured as well (though it may be paler pinkish brown) but contrasts against the dark colour of the shiny corolla by its relative dullness.

In the Worcester-Robertson Karoo and around Montagu, *D. elegans* frequently grows together with *D. caespitosa* subsp. *caespitosa*. South of the Langeberg and Riviersonderend Mountains it has been recorded in several places near where subsp. *vestita* has been collected. In many of these more southern localities, especially around Riversdale but even from Drew to Stormsvlei, it also has a rhizomatous habit with slender, cylindrical stems and cannot be distinguished vegetatively from the more rhizomatous forms of subsp.

vestita. In the Worcester-Robertson Karoo *D. caespitosa* is always distinguishable by its clearly defined annulus, by the tight, longitudinal folding of the corolla lobes and by the corona, which is significantly smaller than the diameter of the annulus and so reveals some of the paler inside of the corolla tube. However, these distinctions break down in the area between Riversdale and Heidelberg and in some localities in this area the corolla is particularly variable. Some flowers are typical of *D. elegans* (with broad corolla lobes and hairs all over the lobes, fig. 3.34), but in others the corolla lobes are more tightly folded and hairs are present on the corolla only in the lower half of the lobes and on the annulus (fig. 3.36). Such material becomes very difficult to separate from '*vestita*' except for the fact that the corolla is shiny and dark-coloured and the outer corona covers most of the annulus. Some material from this area was even described as *D. elegans* var. *seminuda* by N.E. Brown. Meve (1997) recorded

both '*vestita*' and *D. elegans* around Riversdale but all the material recorded from this area (NBG records) appears to be *D. elegans*. The two species are reputed to be distinguishable by their different chromosome numbers ($2n = 22$ for *D. elegans*, $2n = 44$ for *D. caespitosa* according to Meve (1997)) and it would be interesting to know whether this distinction holds up in the Riversdale district.

History

This species, the type of the genus *Duvalia*, was discovered by Francis Masson and depicted in his *Stapeliae Novae*. Identical material was later described by Jacquin as *Stapelia radiata*, despite the fact that this name already existed for plants in the complex around *D. caespitosa* and this confusion took some time to be resolved. Material was first collected in November 1904 just west of Riversdale by N.S. Pillans and this was described as var. *seminuda*.



Fig. 3.35. *D. elegans*, PVB 6699, east of Stormsvlei, on the coastal plain.



Fig. 3.36. *D. elegans*, PVB 7116, Riversdale, on the coastal plain. Here the corolla lobes are especially narrow but they are still shiny and the outer coronal disc is large, as one usually finds in *D. elegans*.

DUVALIA MODESTA

5. *Duvalia modesta*

Duvalia modesta N.E.Br., H. Cap. 4 (J): 1028 (1909).
Type: South Africa, near Aberdeen Road, E Pillans
sub N.S. Pillans 35 (K, holo.; BOL, GRA, iso.).

Duvalia gracilis Meve, *Duvalia*: 75 (1997).
Type: South Africa, 1 km east of Krugerskraal, Meve
346 (K, holo.; NBG, MSUN, iso.).

Dwarf succulent forming mat 40-150 mm diam. *Steins* 10-40 mm long, 7-15 (-20) mm thick, decumbent, very short and compact, green to slightly purplish; *tubercles* 2-4 mm long, conical, fused near bases into 4 (-5) broadly obtuse obscure rows along stem with groove between them, abruptly narrowing into narrowly deltoid leaf-rudiment 1.0-1.5 mm long usually subtended by 2 stipular glands. *Inflorescence* arising around middle of stem, of 1-3 flowers opening in gradual succession; pedicel 8-20 mm long, 10-15 mm thick; *sepals* 2.5-4.0 mm long, 1.0-1.5 mm broad at base. *Corolla* 15-25 mm diam.; outside pale green; inside dull greenish to shiny purplish brown or chocolate, usually becoming paler (and occasionally mottled) towards centre; annulus 1.0-1.5 mm tall, (4.5) 5-8.0 mm broad, $\pm$ circular with sides sloping outwards to lobes or vertically sided, very occasionally mottled with cream, covered with fine papillae < 0.5 mm long; *lobes* 6-9 mm long, 3-6 mm broad at base, tightly folded along midrib at least in upper half and sometimes right to base so deltate- to linear-acute, often with fine hairs 1.0-2.5 mm long near margins in lower two thirds (often absent entirely). *Corona* 3.5-5.5 mm diam., cream to greenish brown or dark purple; *outer lobes* forming disc spreading at or just inside mouth of tube; *inner lobes* 0.5-1.0 mm long, with ascending obtuse dorsal projection < 1 mm long.

Distribution and habitat

Duvalia modesta is mainly known from the Eastern Cape between Graaff-Reinet, Grahamstown and Cradock, with a few collections from near Uitenhage. Collections

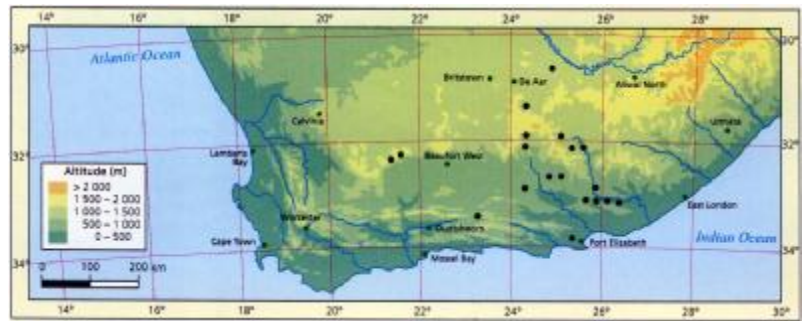


Fig. 3.37. Distribution of *Duvalia modesta*.

made over the past 10 years have shown that it is more widely distributed than this. They have revealed its presence on two farms in the Fraserburg district, between Willowmore and Uniondale as well as near Colesberg and near Richmond in the Great Karoo. This gives it a wide distribution over the central Karoo, the eastern parts of the Little Karoo and into the dry coastal area near Port Elizabeth. The locality cited by Meve (1997) from the former Transkei is considered to refer to *D. caespitosa*.

Plants are generally found under short bushes in flat, gravelly areas and are often inconspicuous, with the stems partly hidden amongst leaf-litter that has accumulated under the sheltering bushlet.

Diagnostic features and relationships

In *D. modesta* the stems are always relatively small and compact, forming fairly dense mats, without any tendency to become rhizomatous. They are roughly four-angled and the tubercles taper into slender leaf-rudiments. The flowers are small, usually chocolate-

brown and the inside varies from shiny to somewhat dull. The lobes are folded along their midribs tightly only in the upper half, while towards their bases they become convex to more or less flat. There are fine hairs near the edges of the lobes and these sometimes extend inwards a little from their sinuses. The annulus is low, usually around 1 mm and at most 1.5 mm tall, often sloping outwards into the lobes but sometimes steep-sided or even very slightly constricted below. It is usually the same colour to slightly paler than the lobes, but occasionally may be markedly paler or even mottled. Even when shiny, the annulus usually has fine papillae on it.

In plants found in the Fraserburg district and between Willowmore and Uniondale, the flowers are never shiny and have a dullish surface which is often yellowish towards the centre with pale brown lobes and the lobes are often tightly longitudinally folded right to their bases. Fine hairs are often still present near the edges of the lobes, but they are very short (< 0.1 mm long) and there are also the short papillae on the annulus that one usually finds in *D. modesta*.

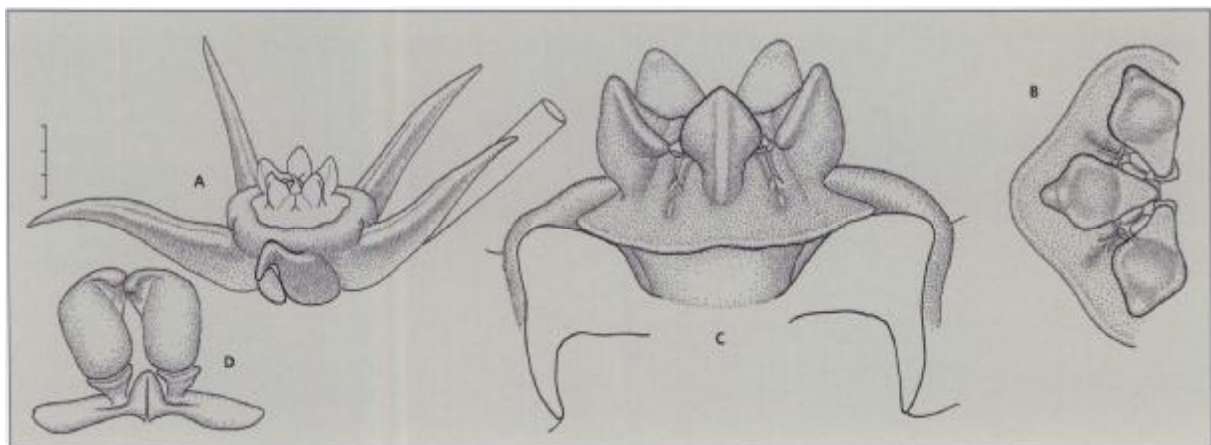


Fig. 3.38. *Duvalia modesta*. A, flower. B, face view of part of gynostegium. C, side view of centre of dissected flower. D, pollinarium. Scale bars: A, 3 mm; B, C, 1 mm (at A); D, 0.25 mm (at A). Drawn from: PVB 3321, east of Richmond.

Plants from around Colesberg and Richmond have flowers with very narrow lobes and some of them have a greenish colour (fig. 3.42) which becomes somewhat paler and faintly spotted with cream on the inside of the annulus. In these the corona is also greenish. Such plants usually grow together with others with pale brown flowers (more typical of *D. modesta*) and they correspond closely to *D. gracilis* Meve.

Like many species, *D. modesta* often grows together with *D. caespitosa*. The plants can usually be distinguished by the smaller, more compact and nearly spherical stems with deeper grooves between the angles and longer, more slender leaf-rudiments in *D. modesta*. Features of the flowers are also useful, especially in those with smaller flowers where the lobes are not tightly folded towards their bases. Since some collections of *D. modesta* do not have the broadened bases of the corolla lobes, the main distinction between them then appears to lie in the height of the annulus: in *D. modesta* the annulus rises less than 1.5 mm above the level

of the bases of the corolla lobes, whereas in *D. caespitosa* the annulus is 2-5 mm tall above the lobes. The flowers are mostly smaller and are more or less glabrous while in *D. caespitosa*, when they are small, they are often covered in the centre with hairs.

History

Duvalia modesta was discovered in June 1902 near Aberdeen Road by Eustace Pillans. White & Sloane (1937) published several good photographs of it that were taken around Somerset East by G.W. Reynolds and one of these collections was figured in the *Flowering Plants of South Africa* (Phillips 1935c). Unlike some other species, there seems to have been little confusion surrounding it.

Recent exploration and interest by local farmers have considerably extended its distribution and shown it to be even more variable than previously thought, so that the recently described *D. gracilis* is now considered to be a form of *D. modesta* as well.



Fig. 3.39. *D. modesta*, PVB 1796a, west of Pearston.



Fig. 3.40. *D. modesta*, PVB 6274, south-west of Fraserburg.



Fig. 3.41. *D. modesta*, PVB 4267, between Uniondale and Willowmore.



Fig. 3.42. *D. modesta*, PVB 3321, east of Richmond. An unusual flower with bright green annulus.



Fig. 3.43. *D. modesta*, PVB 6274, south-west of Fraserburg. A flower with long, narrow lobes folded back right to their bases.



Fig. 3.44. *D. modesta*, PVB 7787, west of Colesberg.



Fig. 3.45. *D. modesta*, PVB 7787, west of Colesberg.



Fig. 3.46. *D. modesta*, PVB 7787, west of Colesberg. This and the previous two pictures show how variable the flowers were in this population.

6. *Duvalia pillansii*

Duvalia pillansii N.E.Br., Fl. Cap. 4 (1): 1026 (1909).

Type: South Africa, near Aberdeen Road, E. Pillans sub *N.S. Pillans* 42 (K, holo.; BM, BOL, GRA, iso.).

Duvalia pillansii var. *albanica* N.E.Br., Fl. Cap. 4 (1): 1027 (1909).

Type: Cape, vicinity of Grahamstown, N.S. Pillans 19 (K, holo.; BOL, GRA, iso.).

Dwarf succulent forming mat 40-150 mm diam. Stems 10-40 mm long, 7-15 mm thick, decumbent, very short and compact to cylindrical, green; *tubercles* 2-5 mm long, conical, fused near bases into 4 (-5) broadly obtuse obscure rows along stem with groove between them, abruptly narrowing into narrowly lanceolate leaf-rudiment (0.5-) 1-2 mm long, usually with very small stipular glands. *Inflorescence* arising from middle to base of stem, of 1-4 flowers opening in gradual succession; *pedicel* 7-15 mm long, 1.0-1.5 mm thick, spreading then ascending to hold flower facing upwards; *sepals* 3-6 mm long, 1.0-1.5 mm broad at base. *Corolla* 20-35 mm diam.; outside purplish green; inside red to shiny purple-brown on lobes changing to cream around edge of tube and inside it; annulus 2.0-2.5 mm tall, 7-10 mm broad, circular, mound-like with sides sloping outwards to lobes, containing outer corona and at least bases of inner lobes, covered with fine papillae < 0.5 mm long; *lobes* 7-14 mm long, 7-8 mm broad at base, longitudinally laxly folded along midrib and only tightly folded near apex so ovate-acute, $\pm$ convex above, with fine purplish hairs 2-3 mm long along margins in lower two thirds. *Corona* 4-5 mm diam., cream to pale yellow; *outer lobes* forming $\pm$ circular disc somewhat below mouth of tube and completely contained in it; *inner lobes* 0.5-1.0 mm long, with spreading to ascending dorsal projection $\pm$ 1 mm long.

Distribution and habitat

Duvalia pillansii is known from a few localities in the Eastern Cape. It has not been seen again in the area around the type locality at Aberdeen Road and the only recent collections are from near Hankey and near Kirkwood, which lie closer to Port Elizabeth and are some 120-150 km from Aberdeen Road.

Around Hankey it grows under small, spiny bushes on sloping, stony ground together with a very rhizomatous form of *D. caespitosa* and numerous other succulents.

Diagnostic features and relationships

Vegetatively *D. pillansii* is not usually distinguishable from *D. modesta* and possesses similar, small, compact stems with relatively long leaf-rudiments.

The flowers in *D. pillansii*, at about 25 mm in diameter, are comparatively large. Inside they are dark purple-brown to red and somewhat shiny on the lobes with this colour fading to become cream on the summit of the annu-



Fig. 3.47. *D. pillansii*, hort. Peckover.

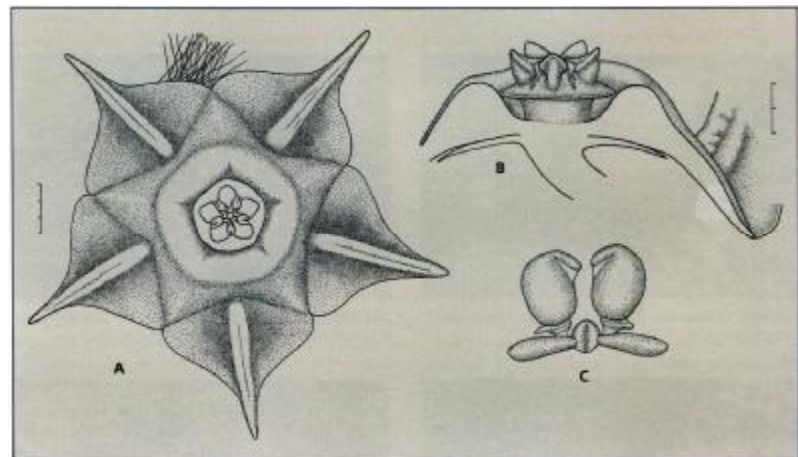


Fig. 3.48. *Duvalia pillansii*. A, face view of flower. B, side view of centre of dissected flower. C, pollinarium. Scale bars: A, 3 mm; B, 2 mm; C, 0.25 mm (at A). Drawn from PVB 7489, Hankey.

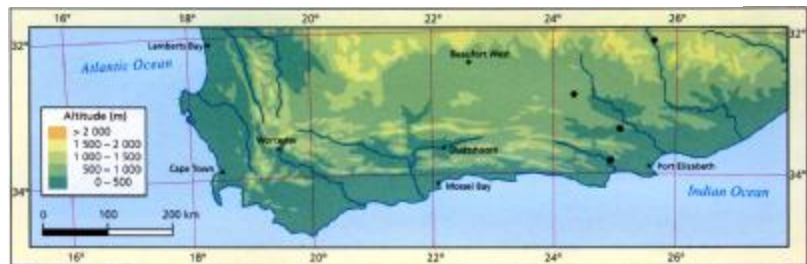


Fig. 3.49. Distribution of *Duvalia pillansii*.

lus and inside the tube. The annulus widens steadily towards the bases of the lobes so that it is mound-like and not steep-sided as in most

of the other southern African species. The other striking difference in the corolla is that the lobes are much less folded longitudinally. In fact only

near their tips are they relatively narrow and for the remainder they are just convex above, with the margins spreading out. As a consequence, the quite long, fine hairs along the margins (which are firmly fixed at their bases and are not at all vibratile) spread out and are clearly visible.

Another unusual feature of *D. pillansii* is the relatively small, yellow outer coronal disc. It is seated from slightly to well below the mouth of the tube. Both this position inside the tube and its colour remind one somewhat of *D. maculata*.

Bayer (1984a) made the suggestion that *D. pillansii* was a large-flowered form of *D. modesta* and noted as well that some of the offspring from self-crosses turned out to resemble *D. modesta*. These observations have not been confirmed (Meve 1997).

History

Duvalia pillansii was discovered by Eustace Pillans near Aberdeen Road in April 1902 in the same area where he later found *D. modesta* and had previously collected *D. maculata*. There are several localities given by White & Sloane (1937) but none seem to have been documented by specimens or photographs. The next recorded collection dates from 1960 (Meve 1997). So few collections have been made that it must still be regarded as the rarest species of *Duvalia* in southern Africa.



Fig. 3.50. *D. pillansii*, PVB 7489, Hankey.

7. *Duvalia maculata*

Duvalia maculata N.E.Br., Fl. Cap. 4 (1): 1033 (1909).

Type: South Africa, near Aberdeen Road, E. Pillans sub N.S. Pillans 3! (K, holo.; BOL, GRA, SAM, iso.).

Duvalia minuta Nel in A.C. White & B. Sloane, Stap., ed. 2, 3:1168(1937).

Type: Namibia, Great Karas Mountains, Mickberg, E.F.T. Rusch (missing).

Lectotype: White & Sloane, Stap., ed. 2, 3: fig. 1218.

Dwarf succulent forming mat 30-150 mm diam. Stems 10-40 (-60) mm long, 6-12 (-18) mm thick, decumbent, mostly short, green to purplish; tubercles 2-5 mm long, conical, fused near base into 4-5 angles along stem, tapering gradually into deltoid acute leaf-rudiment 1-3 mm long subtended by 2 glandular stipular denticles. Inflorescence arising mainly in lower half of stem, of 1-8 flowers developing in fairly rapid succession from small peduncle up to 8 mm long, with numerous bracts 1-2 mm long; pedicel 10-25 mm long, 10-15 mm thick, spreading with erect apex, holding flower facing upwards close to ground; sepals 3-4 mm long, 1mm broad at base. Corolla 15-25 mm diam.; outside pale green to brownish; inside purplish, reddish to yellowish brown, somewhat shiny on lobes; annulus 1.5-2.5 mm tall, 5-8 mm broad, often pentagonal, often heavily indented around rim, somewhat constricted towards base (just above bases of lobes), almost completely containing corona, cream to white speckled with pale brown, covered with fine papillae < 0.5 mm long; lobes 5-10 mm long, 3-5 (-6.5) mm broad at base, often with few short straight hairs up to 2.5 mm long near base, tightly folded along midrib so

linear-acute. Corona 3.0-3.6 mm diam., bright to dull yellow (speckled with brown) to pale orange; outer lobes forming circular to slightly pentagonal disc spreading $\pm$ at level of middle of tube and completely contained in it; inner lobes $\pm$ 0.5 mm long, with obtuse ascending to spreading dorsal horn $\pm$ 1 mm long.

Distribution and habitat

Duvalia maculata is widely but rather diffusely distributed across southern Africa. In Namibia, it is known from four localities. Two are in the Tiras Mountains south-west of Helmeringhausen and the other two lie some 250 km to the south-east, at an altitude of over 2 000 m in the Great Karas Mountains and around their base at about 1 400 m near Griinau. In the Northern Cape it has been found widely from west of Kenhardt to Williston and near Middelpoos, apparently avoiding the flat, pan-like parts of Bushmanland. Further east it is widespread from Fraserburg to Griquastad, Douglas and to Cradock as well as south to Aberdeen Road. There is a single collection from near Fauresmith in the Free State. This distribution is remarkably similar to that of *Ceropegia filiformis* (Bruyns 1995b) and bears some similarity also to that of *Piarranthus cornutus* and *Fockea sinuata*.

Duvalia maculata is usually found in flat areas in stony ground growing under small, karroid bushes. In the western localities it is generally found growing under small, spiny shrublets of *Ruschia spinosa* while further east it grows under small composite shrublets (*Pentzia*, *Pteronia* etc.).

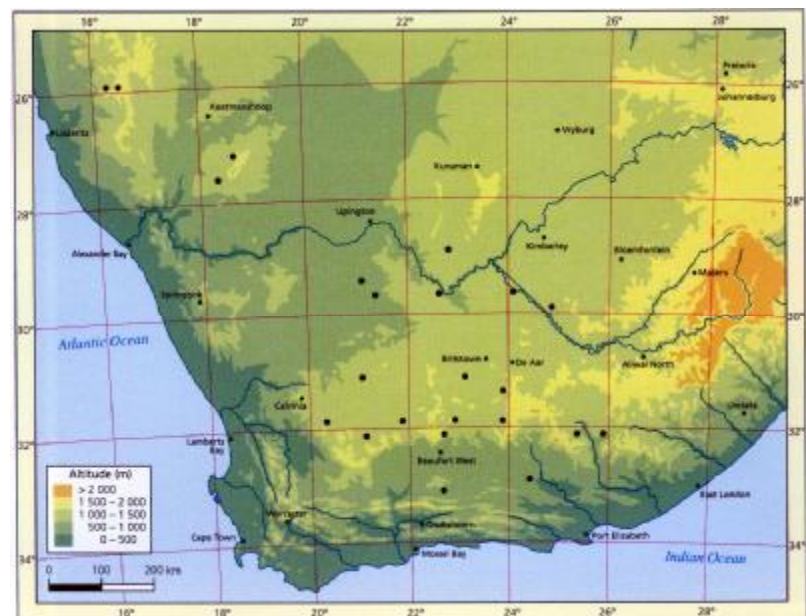


Fig. 3.51. Distribution of *Duvalia maculata*.

DUVALIA MACULATA



Fig. 3.52. *D. maculata*, PVB 5109, north of Victoria West, an unusually soberly-coloured flower.



Fig. 3.53. *D. maculata*, PVB 5109, north of Victoria West, with a particularly pale annulus.

Diagnostic features and relationships

Plants of *D. maculata* usually form small, dense mats of short and compact, roughly four-angled stems (fig. 6) where the tubercles taper into fairly slender leaf-rudiments. Consequently,



Fig. 3.54. *D. maculata*, PVB 6289, east of Middlepos, flower with broad annulus and short lobes.

they could not be separated easily from those of, say, *D. modesta*. However, florally it is quite distinctive.

Flowers are produced in comparatively large numbers on a short, knobby peduncle and they often open in close succession in an inflorescence. The lobes are yellowish to darker

brown (the darker ones are not any different in colour from those in many other species) and are tightly folded for most of their length, with some longitudinal grooves. The very striking annulus, most of which is visible since the corona does not obscure the tube, is characteristically cream to white with brown spots

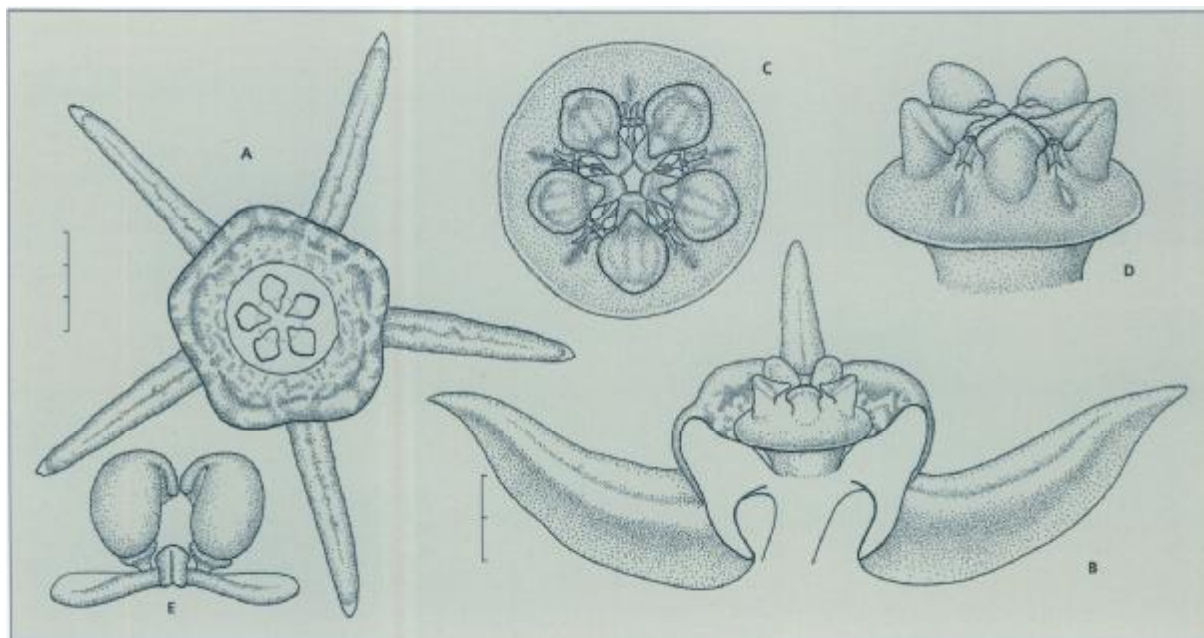


Fig. 3.55. *Duvalia maculata*. A, face view of flower. B, side view of dissected flower. C, face view of gynostegium. D, side view of gynostegium. E, pollinarium. Scale bars: A, 3 mm; B, 2 mm; C, D, 1 mm (at B); E, 0.25 mm (at B). Drawn from PVB 3045, Richmond.

or an irregular, brown mottling. It often has a distinctly undulating margin, with the highest spots alternating with the corolla lobes and it is usually quite a bit broader towards the top than below near the lobes i.e. it is constricted towards the base. The annulus is covered with fine papillae which sometimes give it a velvety appearance.

As in *D. immaculata*, the outer corona is narrower than usual and there is a short stipe so that it sits rather low in the tube and only the inner lobes project from the mouth of the tube. Both the inner and outer lobes are usually bright yellow but pale orange ones have been found and some, from the Tiras Mountains in Namibia, are dull yellow, speckled faintly with brown.

History

Duvalia maculata was discovered by Eustace Pillans in 1900 near Aberdeen Road. There are few early collections, except for some made by E.R. Fuller in the Northern Cape (near Prieska and Hopetown) so it has generally been a poorly known species. In addition, confusion was sown by a figure of *D. caespitosa* which was published in Phillips (1932c) under the name *D. maculata*. This figure was reproduced in White & Sloane (1937: fig. 770) along with another one that was probably made from the same collection (Plate 22), also under *D. maculata*. However, they were aware of the real thing as well, since the redoubtable Sidney Tapscott supplied them with an excellent figure of it (fig. 768) and Ernst FT. Rusch also sent them one from Namibia (fig. 766). Rusch's remarkable collection, which was the first to indicate how widely distributed this



Fig. 3.56. *D. maculata*, PVB 8095, western end of the Tiras Mountains, Namibia.

species is, was made a little before 1936 at the south-western foot of the Great Karas Mountains on the farm Mickberg and was described by Nel as *D. minuta*. This was, until recently, the only record of *D. maculata* from Namibia, although fig. 736 in White & Sloane, also collected by E.F.T. Rusch (but near Aus) might be a further record of it, despite the unusual colouring of the corolla.

Recent collecting has revealed its existence over a wide area in South Africa and, in 1993, it was recollected in Namibia, though considerably further to the west than Rusch's locality. A further trip to Namibia, lasting from December 1999 to January 2000, provided another locality in the Tiras Mountains and, for the first time, showed that it occurred in the Great Karas Mountains as well, where several plants were found growing around the bases of small tufts of grass and among stones near the summit of Lord Hill, at an altitude of over 2 000 m.



Fig. 3.57. *D. maculata*, PVB 8095, western end of the Tiras Mountains, Namibia. Here the outer coronal disc is pale brown rather than the usual yellow and shows considerable difference in colour from the previous picture.

8. *Duvalia immaculata*

Duvalia immaculata (C.A.Lückh.) M.B. Bayer ex L.C. Leach, S. African J. Bot. 55: 268 (1989).

D. maculata var. *immaculata* C.A. Lückh. in A.C.

White & B. Sloane, Stap., ed. 2, 3: 144 (1937).

Lectotype: White & Sloane, Stap., ed. 2, 2: fig. 769.

Dwarf, rhizomatous succulent spreading over 50-300 mm. Stems 20-50 mm long, 5-12 mm thick, decumbent, cylindrical and tessellate to slightly ovoid or clavate, green to brown; tubercles 1-2 mm long, obscure, conical, arranged very roughly into (4-) 5 obtuse and obscure angles along stem, abruptly narrowing into very short acute leaf-rudiment < 1 mm long with microscopic stipular glands. Inflorescence arising mostly in lower half of stem, of 1-6 flowers opening in gradual succession; pedicel 5-25 mm long, 1.0-1.5 mm thick, usually ascending and holding flower facing upwards among stems; sepals 2-3 mm long, 1 mm broad at base. Corolla 17-30 mm diam.; outside brownish green; inside dark chocolate-brown, glabrous but with dull velvety texture; annulus 2-3 mm tall, 7-11 mm broad, often pentagonal, heavily indented around rim and somewhat constricted towards base, forming shallowly bowl-shaped tube, almost completely containing corona, covered with fine papillae < 0.5 mm long; lobes 7-12 mm long, 2-4 mm broad at base, tightly folded along midrib right to base so linear-acute, somewhat rugulose along midrib, glabrous, eciliate. Corona 3-1 mm diam., yellow suffused faintly with brown (particularly on outer lobes); outer lobes forming short pentagonal disc near base of tube and mostly completely contained in it; inner lobes < 1 mm long, obtuse, with spreading broadly obtuse dorsal projection $\pm$ 1 mm long.

Distribution and habitat

Duvalia immaculata occurs along the south coast of the Western Cape from Infanta, near the mouth of the Breede River, eastwards to near the mouth of the Gouritz River and continues eastwards to Klein Brak. All of the known localities are within 50 km of the ocean.

This species usually grows in locally arid spots surrounded by *renosterveld* and *fynbos*. Plants are found on shales and sometimes on limestones and, in the case of limestones, they grow among short bushes and stones, often partly or wholly in the open.

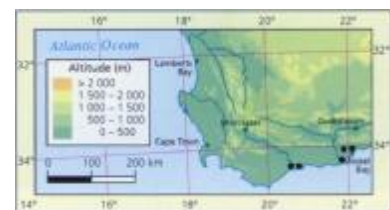


Fig. 3.58. Distribution of *Duvalia immaculata*.

DUVALIA IMMACULATA

Diagnostic features and relationships

The stems in *D. immaculata* have a distinctly rhizomatous habit, often spreading horizontally underground for up to 100 mm before emerging once more to become erect or ascending above the soil. Here the above-ground parts are cylindrical and often rather tessellate, with low, obscure tubercles which are only sometimes joined into angles along the stem and the underground parts are more slender. Meve (1997: 106) suggested that the rhizomatous habit is a response to bush fires. Although fire has played a major role in the evolution and diversification of *fynbos* (Stock & Allsop 1992) and possibly *renosterveld* as well, it is unlikely to have caused species such as this stapeliad to become rhizomatous since the locally arid spots where *D. immaculata* occurs are generally covered with so little vegetation that it would be impossible for them to burn. It is far more likely that this phenomenon is an adaptation to aridity and grazing pressures and, like many features of stapeliads, it appears randomly in species in several different genera. Many of these (e.g. *Tromotriche revoluta* and *T. thudichumii*) are not associated with fire-prone ecosystems.

In *D. immaculata* the corolla is a rich and deep, but not at all shiny chocolate-brown on the lobes and on the annulus. The corolla lobes, which are narrow for their whole length, are usually quite conspicuously longitudinally grooved and somewhat rugulose, especially near the ends. The annulus is rather taller than in *D. maculata*.

In *D. immaculata*, the stipe on which the corona stands is particularly short, at around 0.5 mm, and consequently the corona is very near the base of the tube (fig. 3.59 B). The shallowly bowl-shaped tube varies very much in depth so that sometimes the entire corona is contained within it while on other occasions the inner lobes are still visible above the rim of the annulus. As in *D. angustiloba*, the diameter of the outer coronal disc is more or less the same

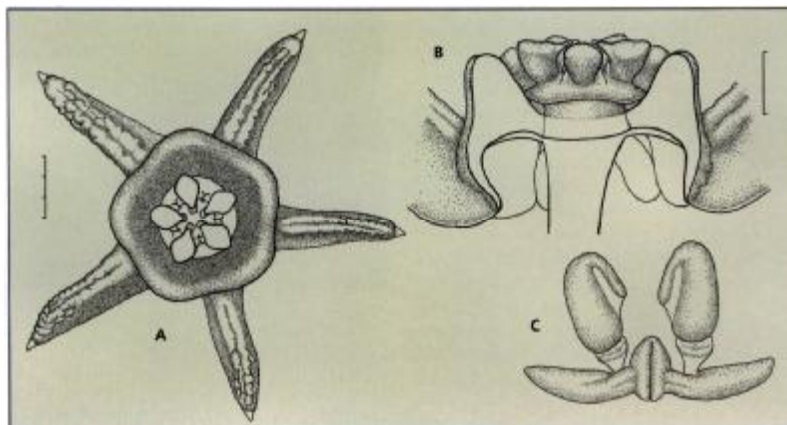


Fig. 3.59. *Duvalia immaculata*. A, face view of flower. B, side view of centre of dissected flower. C, pollinarium. Scale bars: A, 3 mm; B, 2 mm; C, 0.25 mm (at A). Drawn from PVB 7490, Klein Brak.

as the diameter of the top of the corona. The corona is mostly bright yellow. This contrasts strongly with the dark brown of the corolla, even more so than in *D. maculata*, where the corona is also often bright yellow.

History

This species appears to have been discovered by Mrs. Deborah Susanna van der Bijl (née Malan 20 Sept. 1872 - 2 Feb. 1942), who deposited a flowering specimen of it in the Bolus Herbarium in March 1933. Mrs. van der Bijl took a considerable interest in succulent plants, first in the Prince Albert district, where she lived from 1912 till 1928 on the farm Abrahamskraal, and later in the vicinity of Great Brak from 1928 to 1936. The genus *Bijlia* and several species of succulent Aizoaceae as well as the possible hybrid *Stapelia bijliae* were named after her. *D. immaculata* was first mentioned in the literature as the 'immaculate variety' of *D. maculata* in White & Sloane (1937), though two photographs of it appeared in their

earlier version (White & Sloane 1933) under *D. maculata* and it appears to have been well-known to the Lückhoffs before the publication of these volumes. Bayer (1977) was the first to suggest that it was probably a distinct species and the name was finally raised to specific level in 1989 by L.C. Leach.



Fig. 3.60. *D. immaculata*, PVB 7490, Klein Brak.



Fig. 3.61. *D. immaculata*, PVB 7490, Klein Brak. As in *D. maculata*, the corona is yellow, comparatively narrow and deeply sunken into the tube formed by the annulus.



Fig. 3.62. Deborah S. van der Bijl, the discoverer of *Duvalia immaculata*.

9. *Duvalia angustiloba*

Duvalia angustiloba N.E.Br., Gard. Chron. N.S. 20: 230 (1883).

Type: South Africa, from the Karoo, near or on the way to the diamond fields, *Dickson sub Barkly* 33 (K).

Dwarf succulent forming small mat 20-50 mm diam. Stems 8-30 mm long, 6-20 mm thick, decumbent, very short and $\pm$ spherical, green to purplish; *tubercles* 2-4 mm long, conical, fused near base into 4-5 obtuse obscure rows along stem with groove between them, abruptly narrowing into deltoid acute leaf-rudiment 1-2 mm long subtended by 2 stipular glands. *Inflorescence* arising in lower half of stem on short peduncle (< 5 mm long), of 1-20 flowers opening in fairly rapid succession (often 2 or more open at once per inflorescence), bracts deltoid and 1 mm long; *pedicel* 10-40 mm long, 1 mm thick, usually ascending then descending and spreading on ground with upturned apex, holding flower facing upwards; *sepals* 2-3 mm long, 1 mm broad at base. *Corolla* 10-22 mm diam.; outside brownish green; inside red- to chocolate-brown (sometimes this colour speckled on cream to green); annulus 0.4-0.8 mm tall, 3.0-4.5 mm broad, pentagonal, somewhat constricted below, sometimes spotted, covered with fine papillae < 0.5 mm long; *tube* < 1 mm deep; lobes 4-5 mm long, 1.5-2.0 mm broad at base, somewhat longitudinally rugulose, tightly folded along midrib so narrowly linear for whole length and acute, margins with few papillae towards base, eciliate. *Corona* 2-3 mm diam., white to suffused with pink, often with several red-brown patches below inner lobes; outer lobes forming strongly pentagonal disc spreading at or just inside mouth of tube; inner lobes $\pm$ 0.5 mm long, with obtuse spreading dorsal projection $\pm$ 1 mm long.

Distribution and habitat

Duvalia angustiloba is particularly characteristic of the vast, flat plains between Beaufort West, Aberdeen and Rietbron that are known as *Die Vlakke* and lie between 700 and 900 m above sea level. However, my own exploration has shown that it occurs elsewhere too and two collections were made between Victoria West and Loxton,

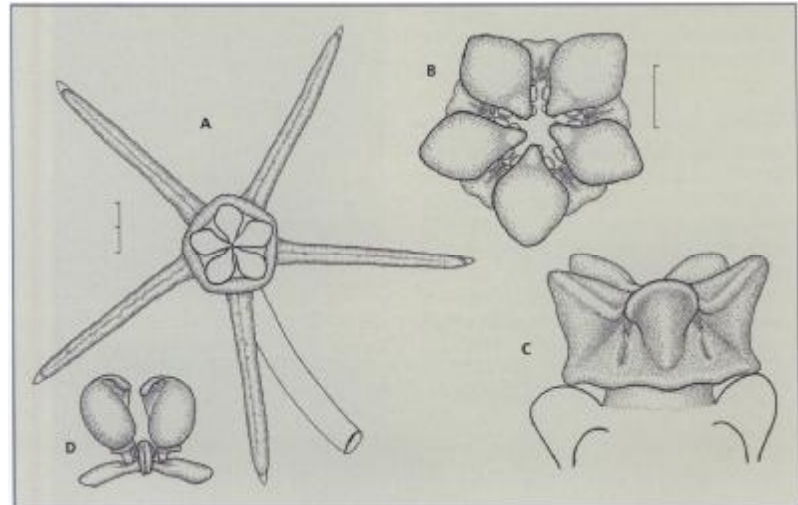


Fig. 3.63. *Duvalia angustiloba*. A, face view of flower. B, face view of gynostegium. C, side view of centre of dissected flower. D, pollinarium. Scale bars: A, 2 mm; B, C, 1 mm (at B); D, 0.25 mm (at B). Drawn from: PVB 2832, east of Beaufort West.

at altitudes of between 1550 and 1750 m.

Mostly plants are found in dry, flat areas of gravel or firm loam, growing under small *Pentzia* bushes or *Lycium* shrubs, though near Loxton it was gathered under small shrubs among dolerite rocks on top of a large, flat-topped mountain.

Diagnostic features and relationships

The stems of *D. angustiloba* form small, tightly packed mats. They are often nearly spherical in outline and are generally short, usually less than 10 mm long. The tubercles are relatively large for the size of the stem and taper into a slender leaf-rudiment but they are not arranged into easily discernible rows.

In *D. angustiloba* the flowers are produced in fairly dense clusters on a short peduncle.



Fig. 3.64. *D. angustiloba*, PVB 8393, near Murraysburg. Dark brown-flowered plants such as this are most typical, though the corolla lobes are faintly mottled here too.

They usually open in quite rapid succession so that a flowering specimen often has plenty of flowers open at once. Like the stems they are also small but they are immediately recognizable in the genus by their extremely slender lobes with an unusually small annulus. Normally the lobes and annulus are deep red or red-brown but flowers are occasionally found where they are brown, mottled with cream to green. The lobes are tightly folded and particularly narrow, with one or more longitudinal grooves along the upper surface.

The corona in *D. angustiloba* is quite large relative to the diameter of the annulus and tends to obscure it somewhat. Most of the corona is white or faintly pink, though there are often some red-brown spots below the inner lobes and around the guide-rials. Consequently its colour contrasts sharply with the dark colour of the corolla. The disc formed by the outer corona is especially small and mostly somewhat hidden

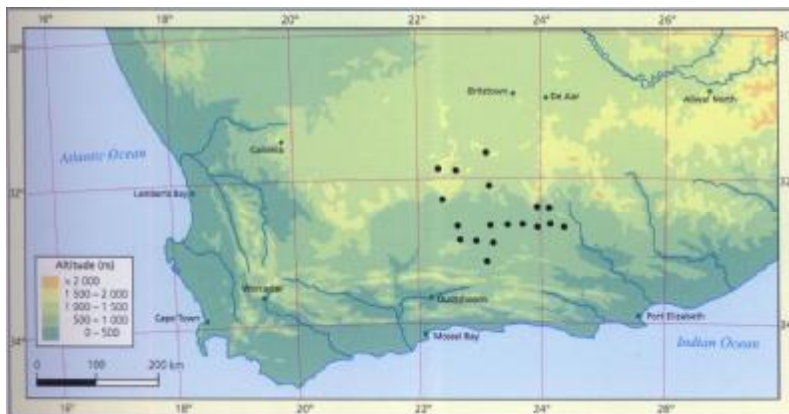


Fig. 3.65. Distribution of *Duvalia angustiloba*.

DUVALIA PARVIFLORA

by the rather larger inner lobes, but it sits more or less on the inner edge of the annulus and covers up the mouth of the very short tube.

History

Duvalia angustiloba was discovered by a Mr. Dickson between 1873 and 1877 (see also *Tridentea virescens*). He brought it to Henry Barkly who, in turn, sent these plants to N.E. Brown at Kew in 1875. They appear to have been cultivated at Kew, for Brown observed its habit of producing remarkable numbers of flowers and was able to make illustrations from live specimens which he published in 1883 and later in Brown (1890) as well.

After this it languished in obscurity and,

although White & Sloane (1937) published photographs of it, they did not have any information as to where it had been found in the wild. In fact, since Dickson's collection there were no recorded gatherings until one from Nelspoort was brought to the Karoo Garden in 1960, though it is not recorded by whom this was collected. In about 1974 it also appeared among some plants of *Piaranthus* that had been gathered between Beaufort West and Aberdeen by M. Bruce Bayer, while he was curator of the Karoo Botanic Garden. These collections gave an indication of where to look for it, since the somewhat enigmatic description of the type locality 'near or on the way to the diamond fields' had not provided significant help in this regard.



Fig. 3.66. *D. angustiloba*, PVB 6673, near Loxton. Here plants had unusually reddish flowers.



Fig. 3.67. *D. angustiloba*, PVB 6682, near Loxton.

10. *Duvalia parviflora*

Duvalia parviflora N.E.Br., Fl. Cap. 4 (1): 1034 (1909).

Type: South Africa, Wittepoort, E. Pillans sub N.S. Pillans 621 (K, holo.; BOL, GRA, iso.).

Dwarf succulent forming mat 40-150 mm diam. Stems 10-25 mm long, 10-15 mm thick, decumbent, ellipsoidal to spherical, pale green to reddish; *tubercles* not distinguishable from surface of stem so that stem $\pm$ without angles to very slightly 4-angled, with minute leaf-rudiment up to 1 mm long subtended by minute stipular glands. *Inflorescence* usually in lower half of stem (occasionally towards apex), of 1-6 flowers developing in gradual succession; *pedicel* 3-10 mm long, 1.0-1.5 mm thick, spreading to ascending, holding flower facing upwards; *sepals* 2-3 mm long, 1 mm broad at base. *Corolla* 10-15 mm diam.; outside creamy green to pinkish; inside cream, sometimes green to pale brown towards tips of lobes but changing to cream towards their bases and on centre; annulus 1-2 mm tall, 3.5-5.0 mm broad, $\pm$ circular, somewhat constricted below (towards bases of lobes), with very fine papillae < 0.5 mm long; *lobes* 3.5-6.0 mm long, 1.5-2.0 mm broad at base, folded along midrib (often not tightly) so linear acuminate to narrowly deltate, somewhat longitudinally rugulose, glabrous, eciliate. *Corona* 3.5-4.0 mm diam., cream to pale yellow; outer lobes forming pentagonal disc spreading at or just inside mouth of tube; inner lobes 0.8-1.0 mm long, obtuse, with ascending-spreading obtuse dorsal projections $\pm$ 1 mm long.

Distribution and habitat

Duvalia parviflora is found only in the Little Karoo. It occurs from about 50 km west of Ladismith eastwards to a little before the steep descent into the Huis River Pass and there are some additional populations east and south of Vanwyksdorp. This range extends over a distance of around 100 km, at altitudes of 200-700 m, making this the most localised species in the genus.

Duvalia parviflora generally grows on flat, stony to loamy ground, under small karroid bushes.

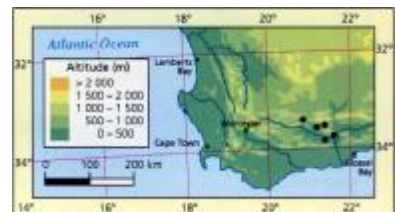


Fig. 3.68. Distribution of *Duvalia parviflora*.

Diagnostic features and relationships

The stems of *D. parviflora* are, at least when turgid, almost completely round and without angles. In seedlings the first few stems are very clearly four-angled and only later does the almost spherical shape without clear angles develop. When the stems are plump one cannot distinguish individual tubercles except for their tiny leaf-rudiments which project straight out of the stem. This situation is quite different to that in any other *Duvalia* but is remarkably similar to what one encounters in some of the western forms of *Piранthus geminatus* and it is even possible occasionally to confuse the two when they are not in flower.

The flowers of *D. parviflora* are also amongst the most distinctive in the genus. The corolla is small and often only 12 mm across. Inside it is generally cream or greenish in the centre on the annulus and on the lower half of the lobes, with this colour changing to greenish or brown towards the tips of the lobes. The corolla lobes vary from tightly to loosely folded along their length so that they are sometimes narrow and sometimes rather broader. They lack marginal cilia entirely. The annulus is fairly small and is only slightly raised above the centre, though it is usually constricted below the rim (fig. 3.71 C).

Both the inner and the outer coronas are pale yellow, matching the colour of the annulus closely, though in fact they are very slightly darker than the annulus. The colour of the corona usually contrasts strongly with the reddish brown of the guide-rails.



Fig. 3.69. *D. parviflora*, PVB 1408, east of Ladismith.



Fig. 3.70. *D. parviflora*, PVB 6305, Outol, west of Ladismith, with paler flowers.

History

Duvalia parviflora was discovered by Eustace Pillans on 5 May 1906 to the west of Ladismith on the road to Laingsburg and it still occurs in the vicinity of where he found it. Meve (1997) cited some material from around Oudtshoorn but this seems to be doubtful since the collections by Scott and Batten that he mentioned were in fact made near Vanwyksdorp rather than around Vanwykskraal, east of Oudtshoorn (Batten, pers. comm. 2000). Consequently these have been excluded from the distribution shown here.

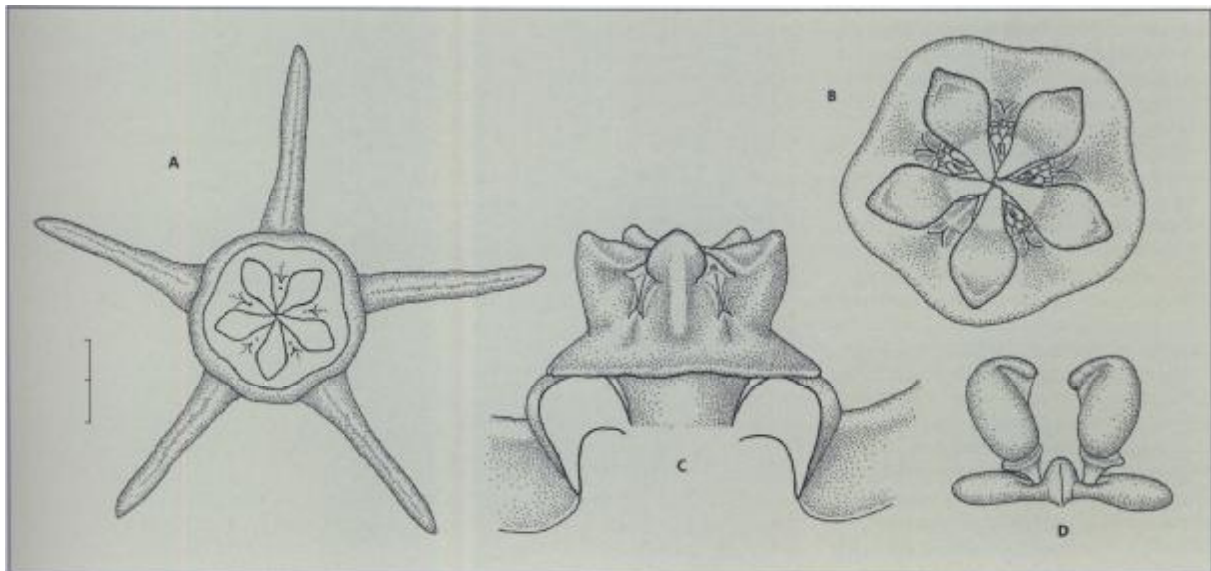
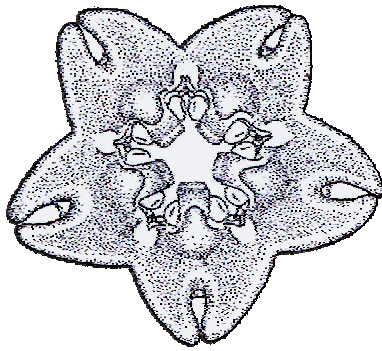


Fig. 3.71. *Duvalia parviflora*. A, face view of flower. B, face view of gynostegium. C, side view of centre of dissected flower. D, pollinarium. Scale bars: A, 2 mm; B, C, 1 mm (at A); D, 0.25 mm (at A). Drawn from PVB 6305, Outol, west of Ladismith.

4. Hoodia



The first species of *Hoodia* known to science was *H. pilifera*. This was gathered by Carl P. Thunberg and Francis Masson in January 1774 in the Karoo beyond Attaquaskloof in the vicinity of the present-day Oudtshoorn and it was described in 1781 as *Stapelia pilifera* by Linnaeus the younger. In 1779, Robert Gordon encountered a *Hoodia* during his journey from Kamieskroon to Pella and Prieska to explore the Orange River. A figure of this, which is reputed to have been made by Gordon, was published by Masson in his *Stapeliae Novae* of 1796-8, where it was described as *Stapelia gordonii*.

In 1826, among his first list of plants cultivated in England, Robert Sweet moved *Stapelia gordonii* of Masson tentatively to *Gonostemon*. He was apparently unhappy about this and, in the second edition of 1830, he moved it to a new genus, *Hoodia*, which he named after a Mr. Hood, a well-known contemporary grower of succulents in Britain. George Don, apparently unaware of Sweet's name, placed *Stapelia gordonii* in a new genus, *Monothylaceum*, in 1837-8. For various reasons the generic names of both Sweet and Don were invalid and *Hoodia* was first validly published by Joseph Decaisne in 1844.

The next person to gather a *Hoodia* was J. Franz Drege, who discovered the rare *H. dregei* in 1827. Somewhat later *H. currorii* was collected by a Royal Navy doctor, A.B. Curror, when his ship stopped in the Bay of Elephants off the Namib Desert in southern Angola in 1840. Material of Curror's *Hoodia* was grown at Kew, where it flowered, and it was on this that Hooker based his genus *Scytanthus* of 1844.

Amongst the material sent by Sir Henry Barkly to N.E. Brown at Kew in the period 1870-7 there were several species of *Hoodia*, including two small-flowered taxa, *H. flava* and probably *H. officinalis*. At much the same time Brown also had an opportunity to examine the stapeliads in Thunberg's herbarium (Brown 1878). There he found the very fragmentary type of *Stapelia pilifera* and he decided to place this in a new genus, *Trichocaulon*, together with these other two small-flowered taxa. He

based this genus largely on Barkly's material of *H. flava*, as the material of *S. pilifera* was inadequate for the compilation of a detailed description. Brown (1890) extended the definition of *Trichocaulon* to include the strange plant described by Willdenow as *Stapelia clavata* as he had, by then, seen a few more collections of similar plants. He placed this species under *Trichocaulon* because, despite the lack of spines on the tubercles, he could find no structural differences in the flowers which would justify its separation from that genus (Brown 1890: *sub t.* 1905).

White & Sloane (1937) listed 18 species of *Hoodia* (along with several more unpublished names). All of these are small to large shrubs along whose stems the tubercles are arranged into many angles and each tubercle is armed with a sharp spine. With the single exception of *H. ruschii*, all of them also had relatively large, saucer-shaped to flat flowers with quite indistinct short and broad lobes, which are abruptly constricted into slender tips.

In their monumental work, White & Sloane (1937) also listed 27 species of *Trichocaulon* (again with several more unpublished names) and this was an altogether more heterogeneous assemblage of species than they catalogued

for *Hoodia*. One of them, *T. decaryi*, came from Madagascar and this was more recently moved to *Stapelianthus* as *S. pilosus*. Another was *T. columnare* which is now *Richtersveldia columnaris*. Subsequent to White & Sloane, the species *T. somaliense* was even described from Somalia, but this is a synonym of *Echidnopsis planiflora*. Of the species enumerated by White & Sloane, two groups were then left. All of them have many-angled stems (with at least 10 angles, though these are often difficult to count). In one group the tubercles taper into a sharp spine and the surface of the stems is smooth. In the other, each tubercle has a small depression at the apex in which a minute, soft leaflet is situated. In these the surface of the stems is papillate. Florally there is little on which these two groups can be distinguished, as was noted by Brown (1890). Plowes (1992) moved the species with spiny stems to *Hoodia*. Among these is the type of *Trichocaulon* (*T. flavum*) and so *Trichocaulon* became a synonym of *Hoodia*. The species without spines were moved to *Lavrancia* (Bruyns 1993) and are now accommodated in a distinct genus, *Laryleachia*.

Hoodia was formerly divided into two sections (Bruyns 1993). However, almost all the characters that were used to separate them

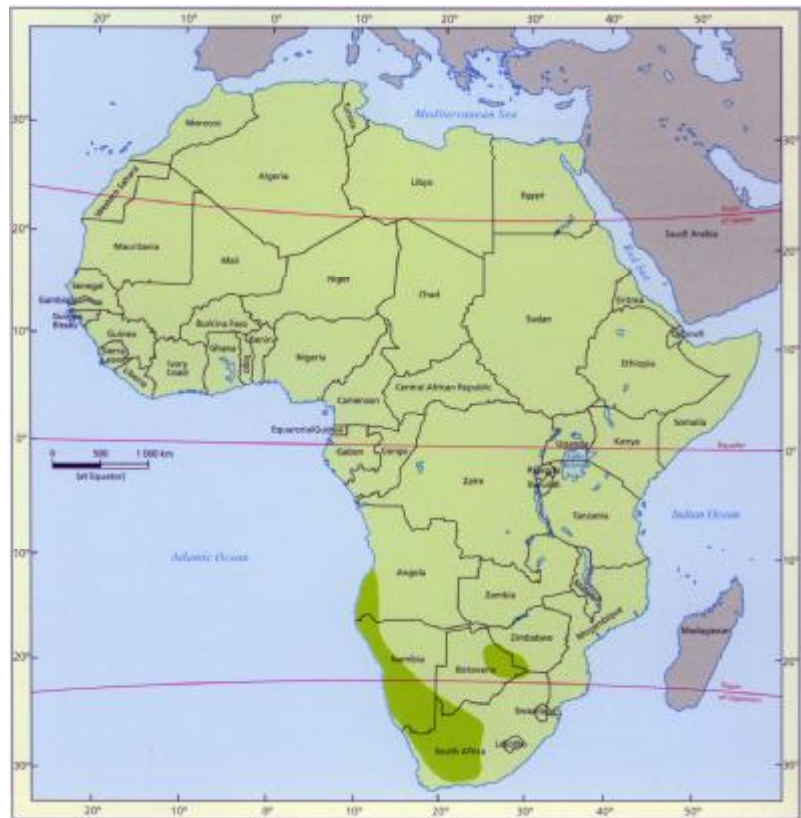


Fig. 4.1. Distribution of *Hoodia*.

had exceptions and this arrangement was not supported phylogenetically so that it is abandoned here.

Hoodia Sweet ex Decne, in DC, *Prodr.* 8: 664 (1844).

Type: *Hoodia gordonii* (Masson) Sweet ex Decne.

Monothylaceum G.Don, *Gen. Hist.* 4: 116 (1837-8),

nom. nud.

Scytanthus Hook., *Hooker's Icon.* Pl. 7: t. 605-6 (1844),

nom. illegit., non *Scytanthus* Meyen (1834).

Type: *Scytanthus currorii* Hook.

Trichocaulon N.E.Br., *J. Linn. Soc. Bot.* 17: 164 (1878).

Type: *Trichocaulon flavum* N.E.Br.

Small to large spiny non-rhizomatous succulent with 3-many stems, forming shrub up to 2 m tall and 2 m broad. Stems 50-2200 mm long, 25-60 (-110) mm thick, erect (rarely prostrate), cylindrical, fleshy and fairly hard, glabrous, grey-green to brown; tubercles 5-15 (-20) mm long, deltoid, laterally flattened and joined into 11-34 obtuse to acute rows along stem, each tipped with a weak to hard sharp spine 3-12 mm long, without stipular denticles. Inflorescences glabrous, 1-30 per stem, arising mainly towards apex of stem (occasionally down to or below middle), each bearing 1-12 flowers opening successively (rarely simultaneously), forming peduncular patches with many narrowly deltoid bracts (often with lateral teeth near base); pedicel 1-60 mm long, 1-6 mm thick, usually spreading; sepals 2-8 mm long, 1-4 mm broad at base, ovate-lanceolate, acuminate. Corolla 8-180 mm diam., rotate to campanulate, small and deeply lobed to large and flat (somewhat plate-like) to shallowly cupular; outside glabrous and smooth; inside glabrous to bristly or finely hairy often with papillae each with an apical bristle; tube (0.5-) 1-8 mm long, 2.5-10 mm broad at mouth, cupular, often with corolla distinctly thickened around mouth. Corona 1-3 mm tall, 2.2-6.0 mm broad, consisting of 2 series arising on staminal tube and partly intergrown, mostly glabrous, sessile to raised on short obtusely pentagonal stipe; outer lobes erect, emarginate or bifid towards apex into ascending lobules, laterally fused with bases of inner lobes and forming small pouch, dorsiventrally flattened and often channelled down inner surface; inner lobes adpressed to backs of anthers and mostly shorter than or equaling them, dorsiventrally flattened, sometimes with small obtuse dorsal projection fused into cup with outer lobes. Anthers horizontal on top of style-head, margins shrinking back to expose pollinia, rectangular. Pollinium D-shaped, longer than broad, insertion-crest twisting from outer edge onto dorsal surface, caudicle attached with $\pm$ broad cupular pad to base. Follicles erect, terete-fusiform, obclavate, slender, consisting of 2 horns diverging at 30-60°, uniformly coloured, glabrous, smooth.

Most species of *Hoodia* have an erect, shrubby habit, with roots developing almost exclusively on the central stem. In *Hoodia alstonii*, *H. currorii*, *H. gordonii* and *H. parviflora* the plant forms a formidable, thorny, cactus-like shrub often a meter or more in height and diameter (in *H. parviflora* sometimes slightly exceeding

2 m tall). In *H. dregei* and *H. juttae* and the small-flowered species the stems rarely exceed 0.5 m tall. Nevertheless, these may still form large clumps which, in the case of *H. pilifera* subsp. *annulata*, may sometimes be as large as 2 m in diameter.

The stems are erect to very shortly decumbent and branch mainly around the base. Each branch has a very short, horizontal portion after which it is erect and parallel to the other branches. The only exception to this is *H. pedicellata* where the stems frequently sprawl with age. They vary very much in thickness, even within a single species. Thus, for example, in *H. gordonii*, the stems are usually 25-35 mm thick in the Ceres Karoo but at the edge of the Namib Desert east of Swakopmund they are up to 50 mm thick. They are thickest in *H. parviflora*, the tallest species in the genus, and here they may be up to 110 mm in diameter near the base. Large plants of this species are by far the most massive of all stapeliads and could be considered to form small trees.

The tubercles on the stems are laterally flattened and joined into long narrow rows running longitudinally up the stem with the channels between these rows much deeper than the grooves between consecutive tubercles in a row. In general in *Hoodia* the thinner-stemmed species have fewer angles per stem (in *H. gordonii* and *H. triebneri* this may be as few as 11) while the thicker-stemmed species have many more (up to 34 in *H. pilifera*). Flowering completely disrupts the arrangement of these angles. In the thinner-stemmed species growth is somewhat faster from one flowering season to the next and so, between bouts of flowering, a portion of stem is produced with regularly arranged tubercles. In the thicker-stemmed species, growth between consecutive flowering seasons is usually small in extent and the angles do not recover their ordered arrangement so that they can be counted only at the base of the stem before the first flowers arise. Each tubercle bears a leaf-rudiment that is modified into a sharp spine. In young seedlings the leaf-like nature of this spine can still be discerned as traces of the blade and midrib can be seen, but this is lost later on. The base of the leaf-rudiment is much swollen, mostly more or less circular in cross-section and it forms a cap-like cover over the summit of the tubercle. Above the basal cap the leaf-rudiment abruptly narrows and then tapers gradually to a finely rounded tip, all the time remaining circular in cross-section. When young, this whole structure is pinkish (often streaked with brown towards the base) to dark brown and is soft and pliable. Soon the leaf-rudiment (including the basal cap) dries out into a sclerified, whitish to brownish spine. Although these spines are normally very hard, they become soft and pliable when moistened as, for example, during a nocturnal mist. In *H. pedicellata* the spines are usually less than 3 mm long and, although

still sharp, they are weak and soon fall off or are worn off by the weathering action of wind-borne sand. This is the only species where they are not persistent.

The surface of the stem in *Hoodia* is generally smooth and the epidermal cells have flat outer walls, although in several cases the seedlings were found to be more papillate, which may hint that the smooth state is derived. On the spines the epidermal cells are particularly long and narrow, running lengthwise along the spine (as in fig. 18 H).

Flowers are borne on both the primary and secondary stems, usually after a few years of growth (this may be as little as 2-3 years in some cases). They are produced near the apex of the stem, usually densely and apparently randomly distributed around its circumference for some distance. When flowering stops, vegetative growth resumes and the stem continues to lengthen and will often produce further flushes of flowers higher up in subsequent years. This alternating of inflorescences and vegetative growth continues and thus the primary and secondary stems may reach a considerable length. In all species, old inflorescences are able to produce flowers in subsequent years but it is the newest inflorescences around the apex of the stem that bear most of the flowers in any given season. The large-flowered species all have few-flowered inflorescences where flowers mature successively. They are borne on a stout pedicel which holds them beyond the spines on the stem. In *H. pedicellata* the pedicel is quite long and holds the flower well away from the stem. In most of the others it is extremely short (1 mm or less) and the flowers are consequently held between the spines and tubercles and are frequently very misshapen. In *H. ruschii* and *H. triebneri* the inflorescence often has several flowers open at once, with many developing from it in one season.

Flowers in *Hoodia* are extremely variable in size, though not to quite the extent that is found in *Stapelia*. The smallest are as little as 8 mm across and the largest reach 180 mm in diameter. As in *Stapelia*, there is relatively little variation in shape.

In the large-flowered species the corolla is funnel-shaped (*H. parviflora*), saucer-shaped to flat with obscure division into five broad but short lobes, each usually with a distinctive, narrow, tail-like tip. Beneath the lobes is a fused area (the 'secondary' tube) which is often flat, as in *H. currorii* and *H. gordonii*, though in these species it may also be bowl-shaped to cupular and it is funnel-shaped in *H. parviflora*. Further towards the centre there is a distinct annular thickening of the corolla, sometimes appearing as a series of slightly raised islands. This annular thickening lies at the mouth of a further, small, central, cupular depression in which the gynostegium is situated, the 'primary' tube. In the small-flowered species the corolla varies from shallowly lobed in *H.*

HOODIA

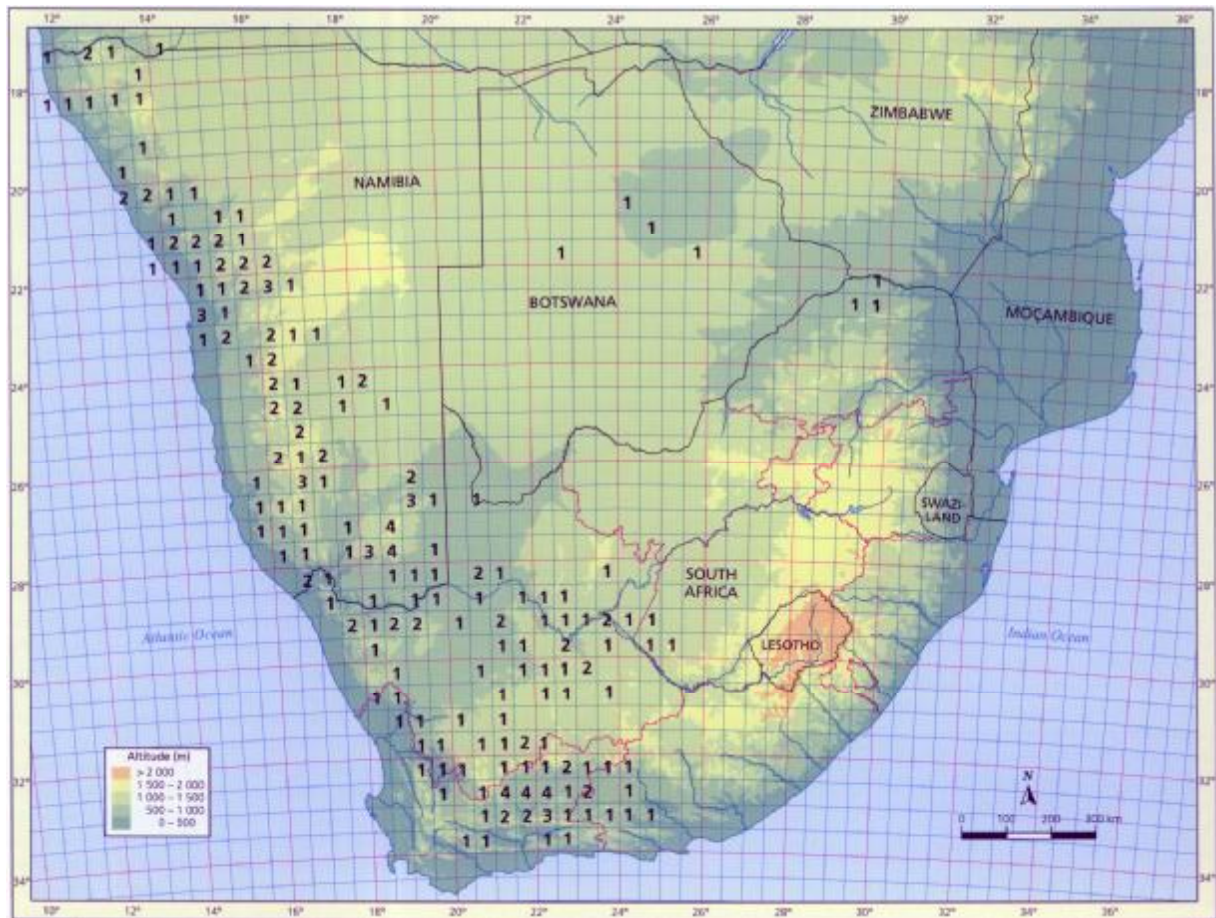


Fig. 4.2. Patterns of diversity in *Hoodia* in southern Africa, showing the number of species recorded to date in each half-degree square.

flava to lobed nearly right to the centre in *H. pedicellata*.

The inside of the corolla varies from smooth (e.g. in *H. juttae* and *H. alstonii*) to variously covered with multicellular, columnar papillae, each tipped with a bristle.

In *Hoodia* the gynostegium is usually raised above the base of the tube on a very short stipe, though this is absent in such species as *H. pedicellata* and is variable in others. Two series of corona lobes are present. Although these are clearly separated in early stages of their development, later the outer series tends to spread out laterally, fusing with the backs of the inner series. This gives rise to a more or less continuous cup around the whole gynostegium, divided into five pockets by the inner lobes. The outer corona lobes are entire and more or less rectangular to shallowly bifid or deeply bifid into relatively prominent, diverging homlets [*H. flava*, *H. alstonii* and *H. pilifera*]. The inner

lobes are always small, flattened and adpressed to the anthers, only slightly longer sometimes in *H. pilifera*.

The pollinia in *Hoodia* are extremely variable, from longer than broad in *H. flava* to unusually broad and short in *H. alstonii*. The corpuscle is small, with minute lateral wings and has a roughly elliptical shape.

Hoodia is found only in southern Africa and the south-western corner of Angola and is confined to arid and very arid regions. It is closely associated with most of the length of the Namib Desert, from around Benguela in southern Angola to south of Lüderitz and also with the valley of the Orange River, along which it extends far to the east (fig. 4.2).

In south-western Angola plants are found from 13°S mainly within 100 km of the coast. In Namibia they are found along the whole length of the western seaboard in a belt which is narrow in the north but broadens out south of the

high region around Windhoek to include most of the arid south. In South Africa *Hoodia* occurs mainly in the Northern Cape in Namaqualand and Bushmanland. A few species come further south across the Great Karoo and onto the Little Karoo, where they reach 33°S, and from the dry western portion of the Free State there are a few records of *H. gordonii* and *H. officinalis*. The very isolated *H. currorii* subsp. *lugardii* occurs in a small area in the Limpopo Province (South Africa) and is the only species recorded from Botswana and Zimbabwe.

Hoodia gordonii and *H. currorii* cover almost the whole distribution of the genus (*H. gordonii* is absent in the Little Karoo and some of the higher areas on the escarpment) and these two are sympatric in a small area only, from the Brandberg to Karibib in central Namibia. *Hoodia parviflora*, which is closely related to *H. currorii*, is more local to the mountains of south-western Angola and

north-western Namibia and occurs just adjacent to *H. currorii*. *Hoodia dregei* and *H. juttae* are very local and grow within the distribution area of *H. gordonii*, to which both are closely allied. Among the small-flowered species, the situation is more complex and the two widely distributed species are *H. flava* and *H. officinalis*. The quite widely distributed *H. pedicellata* and the very local *H. ruschii* and *H. triebneri* are to some extent associated with the distribution area of *H. officinalis*. *Hoodia alstonii* and *H. pilifera* occur around the edges of the distribution area of *H. flava*. *Hoodia pilifera* subsp. *pilifera* and *H. alstonii* occur mainly within the winter-rainfall belt of the Western Cape, Northern Cape and Namibia, and *H. officinalis* subsp. *delatiana* occurs exclusively within it. All the others occur in the summer-rainfall region. In a few areas the number of species per half-degree square rises to four (the Great Karas Mountains, the Great Karoo south of Beaufort West) and this is where two large-flowered species are found together with two small-flowered

species. In the Great Karas Mountains, one of these is a local endemic (*H. juttae*) and in the Great Karoo *H. dregei* is similarly local. In fact, *Hoodia* possesses a surprising number of local species and all of *H. dregei*, *H. juttae*, *H. ruschii* and *H. triebneri* occur over a restricted range.

Key to the species

1. Pedicel 2-6 mm thick, flowers (20-) 25-170 mm diam., never dark red-brown to purple-black, mostly saucer-shaped with broad flat to bowl-shaped united part (rarely funnel-shaped), with small tube just enclosing gynostegium, lobes much less than half as long as broad (excluding narrow tip) and shorter than breadth of united part of corolla outside corolla-tube 2.
2. Corolla glabrous 3.
3. Corolla 20-55 mm diam., limb of outer corona adpressed to corolla just outside tube 10. *H. juttae*
3. Corolla (40-) 50-100 mm diam., outer corona just touching side of corolla tube near mouth, not adpressed to corolla outside tube 9. *H. gordonii*
2. Corolla covered with fine hair-like bristles 4.
4. Outer corona lobes not exceeding height of inner lobes 5.
5. Corolla 28-48 mm diam., inside densely covered with soft white hair-like bristles obscuring colour of surface, outer corona lobes touching surface of corolla outside tube 11. *H. dregei*
5. Corolla (40-) 50-100 mm diam., bristles inside neither dense nor obscuring colour of surface, outer corona touching corolla tube near mouth and not outside tube 9. *H. gordonii*
4. Outer corona lobes exceeding height of inner lobes 6.
6. Corolla funnel-shaped, usually yellow or orange, stems matt bluish green 13. *H. parviflora*
6. Corolla bowl-shaped to flat, brick-red to flesh-pink, stems grey-green to brownish green 12. *H. currorii*
1. Pedicel 0.5-1.5 (-2) mm thick, flowers 8-20 mm diam., if larger (20-40 mm) then dark red-brown to purple-black, if saucer-like then without small tube enclosing gynostegium, lobes more than half as long as broad and much longer than breadth of united part of corolla outside tube 7.
7. Horns of outer corona lobes adherent laterally to dorsal part of inner lobes for entire length of outer lobes 8.
8. Corona 2.0-2.2 mm broad across top, corolla tube conical with sides of tube touching sides of gynostegium 9.
9. Stems 22-28-angled, corolla 20-40 mm diam. 7. *H. ruschii*
9. Stems 12-14 (-16)-angled, corolla 11-15 mm diam. 8. *H. triebneri*
8. Corona 3-4 mm broad across top, corolla tube saucer-shaped, sides of tube not touching sides of gynostegium 2. *H. officinalis*
7. Horns of outer corona lobes not adherent laterally to dorsal part of inner lobes for more than half of length of outer lobes 10.
10. Stems usually sprawling, spines only present on young growth, pedicel 4-15 mm long, flowers never yellow inside 1. *H. pedicellata*
10. Stems erect with persistent spines, pedicel 2 mm long or shorter (if slightly longer then flowers bright yellow inside) 11.
11. Corolla tube 2-4 mm deep and completely containing gynostegium (except sometimes for tips of outer corona lobes), united part of corolla flat to funnel-shaped 12.
12. Corolla densely papillate inside, corolla tube cupular, pollinia longer than broad 13.
13. Corolla ± without raised annulus around mouth of tube, inside pale yellow, greenish yellow to pinkish, corona yellow 6. *H. grandis*
13. Corolla with raised annulus around mouth of tube, inside purple-brown or black to pinkish brown, corona dark purple-brown or purple-black 5. *H. pilifera*
12. Corolla smooth inside, corolla tube broadly conical, pollinia broader than long 4. *H. alstonii*
11. Corolla tube < 1 mm deep and containing only basal stipe of gynostegium, united part of corolla flat to slightly saucer-shaped 3. *H. flava*

HOODIA PEDICELLATA

1. *Hoodia pedicellata*

Hoodia pedicellata (Schinz) Plowes, *Asklepios* 56: 9 (1992).

Trichocaulon pedicellatum Schinz., *Verh. Bot. Vereins Prov. Brandenburg* 30: 266 (1888).

Type: Namibia, probably near Hope Mine, Stapf (K).

Sprawling succulent with up to 20 or more stems. Stems erect when young, later sprawling, 100-250 (-500) mm long, 25-50 mm thick; *tubercles* conical, arranged into 1-20 obtuse rows along stem, each tipped by a dark spine 1.5-3.0 mm long (soon weathered off by sand so that spines usually only found at growing tip of stem). *Inflorences* each with 1-4 flowers; *pedicel* 4-15 mm long, 0.5-1.0 mm thick, descending and holding flower facing downwards; *sepals* 1.5-2.0 mm long, lanceolate, acuminate. *Corolla* rotate, lobed nearly right to centre, 8-14 mm diam.; inside maroon or light to dark purple-brown, without papillae; *tube* usually < 1 mm long, just enclosing base of corona, formed by 5 thickened bulges in corolla just below sinuses of lobes; *lobes* ascending to spreading, 3-6 mm long, 2.5-3.0 mm broad at base, ovate-lanceolate, acuminate, margins recurved so that inside noticeably convex. *Corona* 1.5-2.0 mm tall, 3.0-3.5 mm broad, purple-brown or yellow, glabrous, raised on short stipe; *outer lobes* 0.7-1.5 mm long, spreading, bifid

nearly right to base into widely diverging lobules, laterally fused to bases of inner lobes at least in lower half; *inner lobes* $\pm$ 0.4-1.0 mm long, sometimes exceeding anthers, linear, obtuse, with narrow dorsal ridge near base joined to outer lobes.

Distribution and habitat

Hoodia pedicellata occurs exclusively in the coastal mist-belt of the tropical Namib Desert from slightly south of Swakopmund to at least as far as a little north of Foz do Cunene in south-western Angola. It seems to be found only within 80 km of the coast. The southern portion of the distribution is well documented but beyond the mouth of the Ugab River little is known and it may be much more common than the few records indicate.

Diagnostic features and relationships

In *H. pedicellata* the stems often sprawl among rocks and may even be pendulous, as in the exceptionally large plant shown by Giess (1981). The spines are usually found only near the growing apex of the stem as they are weak and

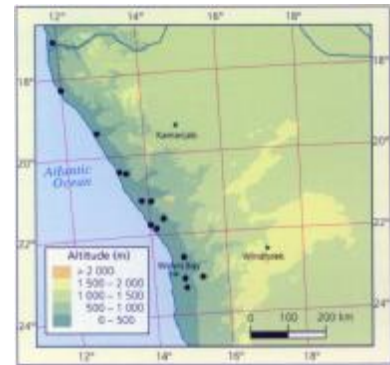


Fig. 4.3. Distribution of *Hoodia pedicellata*

soon weathered off by wind-blown sand, with the result that the tubercle rapidly becomes spineless. Stems which are spineless bear some resemblance to those of *Larrryleachia*. White & Sloane (1937: 991, 1014) used this resemblance to suggest that this species represents an intermediate between the 'spiny' *Trichocaulons* and the 'spineless' species. This hypothesis is

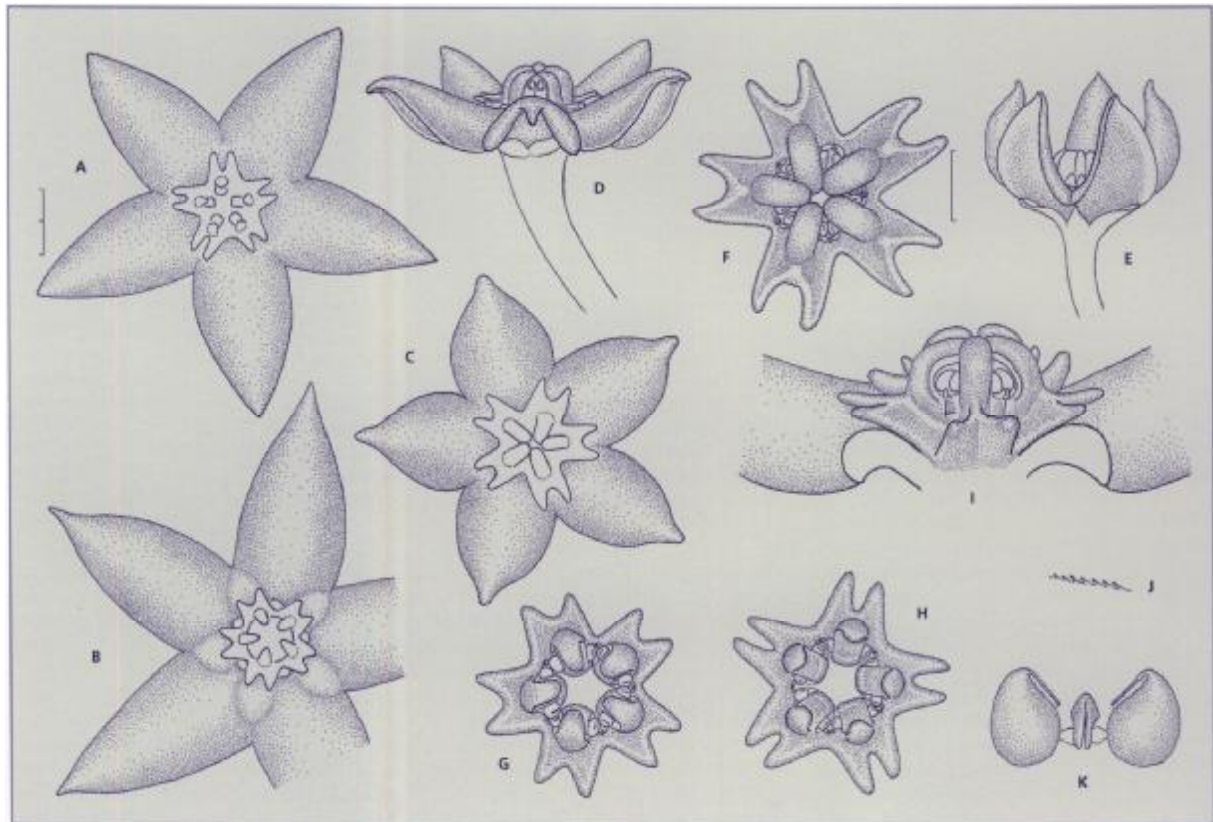


Fig. 4.4. *Hoodia pedicellata*. A-C, face view of flower. D, E, side view of flower. F-H, face view of gynostegium. I, side view of gynostegium and centre of dissected flower. J, papillae inside corolla lobes. K, pollinarium. Scale bars: A-E, 2 mm (at A); F-I, 1 mm (at F); J, 0.5 mm (at F); K, 0.25 mm (at F). Drawn from: A, C, D, F, H, I, M. Visagie, north of Swakopmund, Namibia; B, G, Codd 10585 (PRE); E, J, Cape Cross, Namibia (PRE).

clearly wrong since in *H. pedicellata* seedlings and all young, growing shoots show the spines typical of *Hoodia*.

The flowers of *H. pedicellata* (and of *H. mossamedensis* from Angola) are remarkable for their nodding habit on the end of relatively long pedicels which keep the flowers from being distorted by pressure from the neighbouring spines and tubercles. In *H. pedicellata* the flowers are particularly deeply lobed and the lobes are mostly relatively narrow with the margins folded well back. On the inside they have a velvety texture caused by a covering of very fine papillae and a beautiful, dark, maroon to purple-brown colour. The flowers are variable in size and the extent to which the lobes spread out.

There is hardly any tube in the centre of the corolla and the gynostegium is more or less fully exposed. The outer corona lobes spread out just above the surface of the corolla and, as in the next species, are deeply incised below the guide-rails with the lobules from adjacent lobes gathered behind the anther and the inner lobe.

Hoodia pedicellata is probably most closely related to *H. mossamedensis* from Angola with which it shares the remarkably long pedicels. Both have a similar coronal structure to *H. officinalis*, *H. ruschii* and *H. triebneri*. *Hoodia pedicellata* differs from all of them in the stems: in the others these are erect and more persistently spiny with the tubercles laterally flattened and joined into angles, whereas in *H. pedicellata* the tubercles are conical and only joined together at the base and arranged (but not fused) into rows along the stem. Apart from the differences in the stems, *H. mossamedensis* is distinguished mainly by the differently shaped corolla lobes

(more deltate than lanceolate), the deeper tube with thickened mouth which contains most of the gynostegium, the slightly larger papillae on the corolla (each with an obvious apical bristle) and the only very slightly divided, much shorter outer corona lobes. In *H. pedicellata* the inner corona lobes and anthers rise up much higher above the level of the outer corona lobes.

History

Hoodia pedicellata was discovered by the geologist Friedrich M. Stapf (or Stapff) in 1885 or 1886 when he visited the Hope Mine near Swakopmund.

Dinter observed it in the same area soon afterwards. The only known collection from Angola was made by Eduardo J. Mendes near Espinheira, north of the mouth of the Kunene River.



Fig. 4.5. *H. pedicellata*, E. Erb, near Rossing, Namibia.



Fig. 4.6. *H. pedicellata*, PVB 8071, north-east of Cape Cross, Namibia, plant growing out from beneath a rock on a low ridge, December 1999.

2. Hoodia officinalis

Hoodia officinalis (N.E.Br.) Plowes, Asklepios 56: 9 (1992).

Trichocaulon officinale N.E.Br., Bull. Misc. Inform. 1895: 264 (1895).

Type: South Africa, Cape (Bechuanaland), material imported to America as remedy for piles, some slices of stem with flowers attached presented to Kew by Mr. E.M. Holmes of the Pharmaceutical Society (K).

Shrub with 3-many stems, up to 0.3-0.4 m tall and 0.5 (-1.0) m broad but mostly much smaller. Stems 0.1-0.4 m tall, 35-70 mm thick, erect to sprawling; tubercles joined in lower half into (4-)17-23 obtuse angles, each tipped with sharp brown spine 4-12 mm long. Inflorescences each with 1-3 flowers; pedicel 0.5-2.0 mm long, 0.5-1.0 mm thick; sepals (1.0-) 2.0-3.5 mm long, 1.0-1.5 mm broad at base, ovate-lanceolate, acuminate. Corolla 10-20 mm diam., rotate to broadly campanulate; outside pale green with brownish veins to reddish brown; inside red-brown to yellow-brown often with tube much paler yellow, with dense to scattered covering of small conical obtuse papillae (rarely entirely smooth) each tipped with a fine bristle; tube 2-3 mm deep, broadly saucer-shaped, slightly thickened towards base; lobes 3-6 mm long, 3.5-7.0 mm broad at base, ascending with recurved tips, ovate-deltate, acuminate. Corona 1.5-2.0 mm tall, 3-4 mm broad, yellow to dark red-brown, finely pubescent on outside to glabrous, raised on very short stipe; outer lobes $\pm$ 1 mm long, erect, bifid down middle nearly to base into obtuse erect teeth, laterally fused to bases of inner lobes for most of length to form pouch; inner lobes < 0.5 mm long and $\pm$ half as long as anthers, deltoid, obtuse, with broad obtuse dorsal projection near base joined laterally to outer lobes.

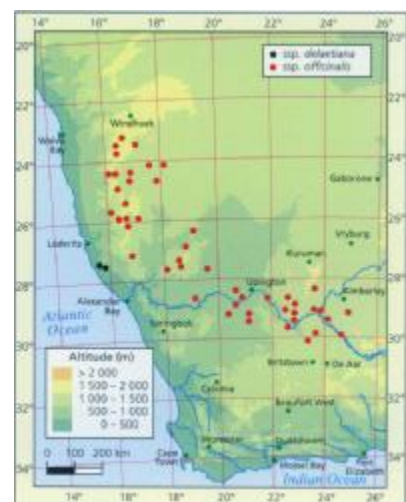


Fig. 4.7. Distribution of *Hoodia officinalis*.

HOODIA OFFICINALIS

Key to the subspecies of <i>H. officinalis</i>	
Corolla 10–14 mm diam., inside densely covered with small papillae	2a. subsp. <i>officinalis</i>
Corolla 14–20 mm diam., inside with very few scattered papillae or smooth	2b. subsp. <i>delatiana</i>



Fig. 4.8. *H. officinalis* subsp. *officinalis*, PVB 3570, south of Koes, Namibia.



Fig. 4.9. *H. officinalis* subsp. *officinalis*, PVB 3179, Tiras Mountains, Namibia.

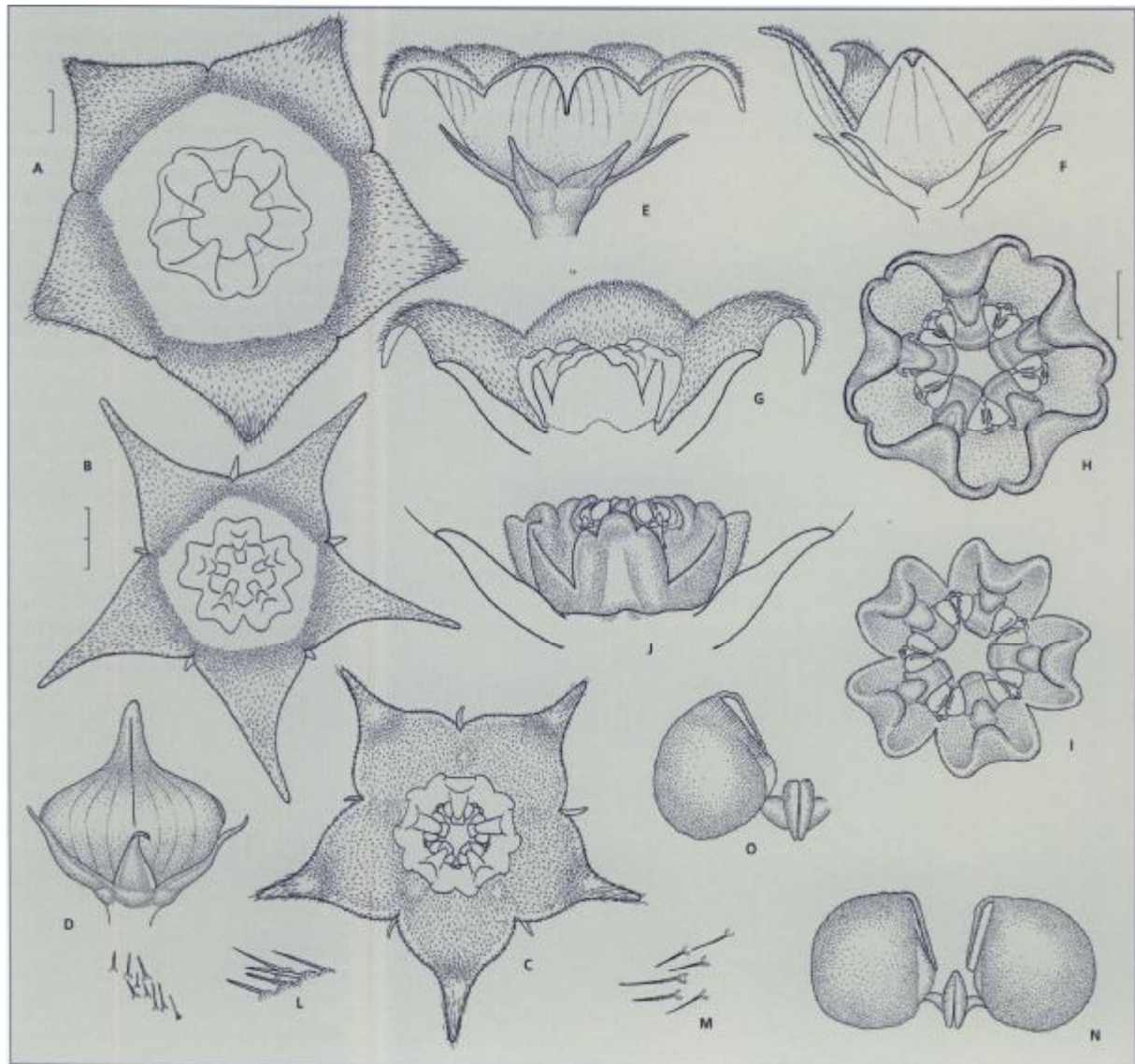


Fig. 4.10. *Hoodia officinalis* subsp. *officinalis*. A-C, face view of flower. D, bud. E, F, side view of flower. G, side view of dissected flower. H, I, face view of gynostegium. J, side view of gynostegium. K-M, papillae inside corolla: K in base of tube; L, M, at end of lobes. N, O, pollinarium. Scale bars: A, G, 1 mm (at A); B-F, 2 mm (at B); H-J, 1 mm (at H); K-M, 0.5 mm (at H); N, O, 0.25 mm (at H). Drawn from: A, E, G, H, O, Kratz, south-east of Gamsberg, Namibia; B, I-K, N, PVB 1511, Nabibis, Tiras Mountains, Namibia; C, D, F, PVB 3179, Tiras Mountains, Namibia; L, PVB 3570, south of Koes, Namibia; M, PVB 3069, Kloof, Prieska.

2a. *Hoodia officinalis* subsp. *officinalis*

Trichocaulon rusticum N.E.Br., Fl. Cap. 4 (1): 891 (1909). *Hoodia rustica* (N.E.Br.) Plowes, Asklepios 56:10 (1992).

Type: South Africa, Kenhardt, Marloth 3764 (missing).

Trichocaulon pubiflorum Dinter, Feddes Rept. Spec. Nov. Regni Veg. 30:192 (1932).

Type: Namibia, Velloor, east of Warmbad, 29 Mar. 1924, Dinter (missing).

Shrub up to 0.3 m tall and 0.5 (-) m broad but mostly much smaller. Stems 35-65 mm thick, erect, tubercles joined into (4-) 17-22 angles, each tipped with brown spine 4-6 mm long. Pedicel mostly < 1 mm long; sepals 2.5-3.5 mm long, 1 mm broad at base. Corolla 10-14 mm diam., rotate to somewhat campanulate; outside pale green with brownish veins; inside red-brown to yellow-brown with tube much paler and yellowish behind corona, covered with small conical obtuse papillae each tipped with a fine bristle; lobes 3-5 mm long, 3.5-5.5 mm broad at base. Corona $\pm$ 1.5-2.0 mm tall, 4 mm broad, mostly yellow, sometimes suffused with fine red dots and inner lobes brownish, usually finely pubescent on outside.

Distribution and habitat

Hoodia officinalis subsp. *officinalis* is the most widespread taxon among the small-flowered species of *Hoodia*. It occurs from a little south of Windhoek more or less throughout southern Namibia, except in the south-western winter-rainfall area and in the deep sands of the Kalahari in the east. Outside Namibia it is found eastwards across the Northern Cape to Griqualand West near Douglas and Kimberley and it just enters the western part of the Free State at Jacobsdal (with one imprecisely recorded collection from further east near Phillipstown).

Only in one locality (just south of the Naukluft in Namibia) was it found to be plentiful. Mostly it is of sporadic occurrence, though it is not necessarily rare. Plants are almost always found growing inside bushes in flattish or gently sloping areas and they are often associated with patches of the *driedoring*, *Rhigozum trichotomum*.

Diagnostic features and relationships

Specimens of this subspecies vary very much in the size and thickness of the stems. The largest (with stems up to 300 mm tall and 65 mm thick, which formed robust shrubs up to 1 m in diameter) were seen in a year of good rainfall in the Aroab district of south-eastern Namibia. These were exceptional and mostly the stems are much smaller (usually around 150 mm tall) and only 35-50 mm thick.

In subsp. *officinalis* the flowers are small



Fig. 4.11. *H. officinalis* subsp. *officinalis*, PVB 4528, near Olifantshoek.

and inconspicuous. The corolla is variable in colour from a deep, pinkish brown to yellow-brown and it usually has a paler whitish to yellowish centre behind and around the gynostegium. The corolla lobes are also somewhat variable in shape and especially around the Tiras Mountains (e.g. fig. 4.9) they have rather longer, more acuminate tips than elsewhere, where they tend to be more shortly acute. On the inside the lobes will often be observed to have a silvery sheen towards their tips and this is caused by the bristles on the apex of each papilla on the surface being almost horizontal in these parts. Elsewhere, (for they cover nearly the entire inside of the corolla) they are more erect and are not easily visible to the naked eye.

The corona varies from deep, bright yellow to pale yellow. This structure is situated in a bowl-shaped depression in the centre of the flower. It consists of outer lobes which are deeply incised opposite the guide-rails, with small rounded lobules that are fused laterally to the backs of the inner lobes. The inner lobes are tiny and do not equal the anthers. A curious feature of the corona is the small, crystalline, sharp-tipped, colorless to reddish hairs found on the outside usually especially densely below

the backs of the inner lobes. This has been observed in specimens throughout southern Namibia but not in any South African material. This phenomenon is seen also occasionally in *H. currorii*.

The stems of subsp. *officinalis* have slightly fewer rows of broader, more rounded (less laterally flattened) tubercles with slightly stouter, darker spines than in *H. flava*. Thus, although these two are vegetatively similar they can actually be distinguished without flowers. However, when flowers do appear there is no confusing them at all. *Hoodia flava* has a virtually flat flower with mandible-like outer corona lobes and it lacks the 'pubescence' of subsp. *officinalis*.

The respective distributions of these two species are curiously superimposed: in southern Namibia and Bushmanland *H. flava* actually crosses over the distribution range of *H. officinalis*. Nevertheless, there are no known localities where they occur together and *H. officinalis* seems to be absent in the area from the eastern flank of the Great Karas Mountains to Pofadder where *H. flava* occurs.

History

Subsp. *officinalis* was described from material sent from the northern Cape Province in South Africa and presented to Kew in 1889. This came from a region formerly included in the British colony of Bechuanaland, some of which is now Botswana, but it is not known precisely when or where this material was collected. Other material which almost certainly belonged to subsp. *officinalis* was sent to Kew before 1877 by Henry Barkly and this had been found along the Vaal River (Brown 1890). Plants were first collected in Namibia by Dinter in April 1911 on the farm Nontsas, near Maltahöhe (Dinter 1921: 53).



Fig. 4.12. *H. officinalis* subsp. *officinalis*, PVB 5128, just west of Strydenburg.

2b. *Hoodia officinalis* subsp. *deletaiana*

Hoodia officinalis subsp. *deletaiana* (Dinter)

Bruyns, Bot. Jahrb. Syst. 115: 216 (1993).

Trichocaulon delaetianum Dinter, Feddes Reperit. Spec. Nov. Regni Veg. 19:155 (1923).

Hoodia delaetiana (Dinter) Plowes, Asklepios 56: 8 (1992) as '*deletaeti*'.

Type: Namibia, Klinghardt Mountains, Dinter 4735 (missing).

Neotype: Namibia, Klinghardt Mountains, Merxmüller & Gies 32150 (WIND, holo.; M, iso.).

Shrub to 0.4 m tall and 0.6 m broad. Stems 40-70 mm thick, erect to sprawling; *tubercles* fused into 19-23 obtuse angles, each tipped with sharp brown spine up to 12 mm long. *Pedice*l 1-2 mm long; *sepals* (10-) 2.0-2.5 mm long, $\pm$ 1.5 mm broad at base. *Corolla* (12-) 14-20 mm diam., broadly campanulate; outside reddish brown; inside brownish yellow to yellow, with few scattered papillae or smooth; *lobes* 4-6 mm long, 5-7 mm broad at base. *Corona* 1.5-2.0 mm tall, 3.0-3.5 mm broad, dark red-brown to reddish, glabrous.



Fig. 4.13. *H. officinalis* subsp. *deletaiana*, PVB 7903, Klinghardt Mountains, Namibia.

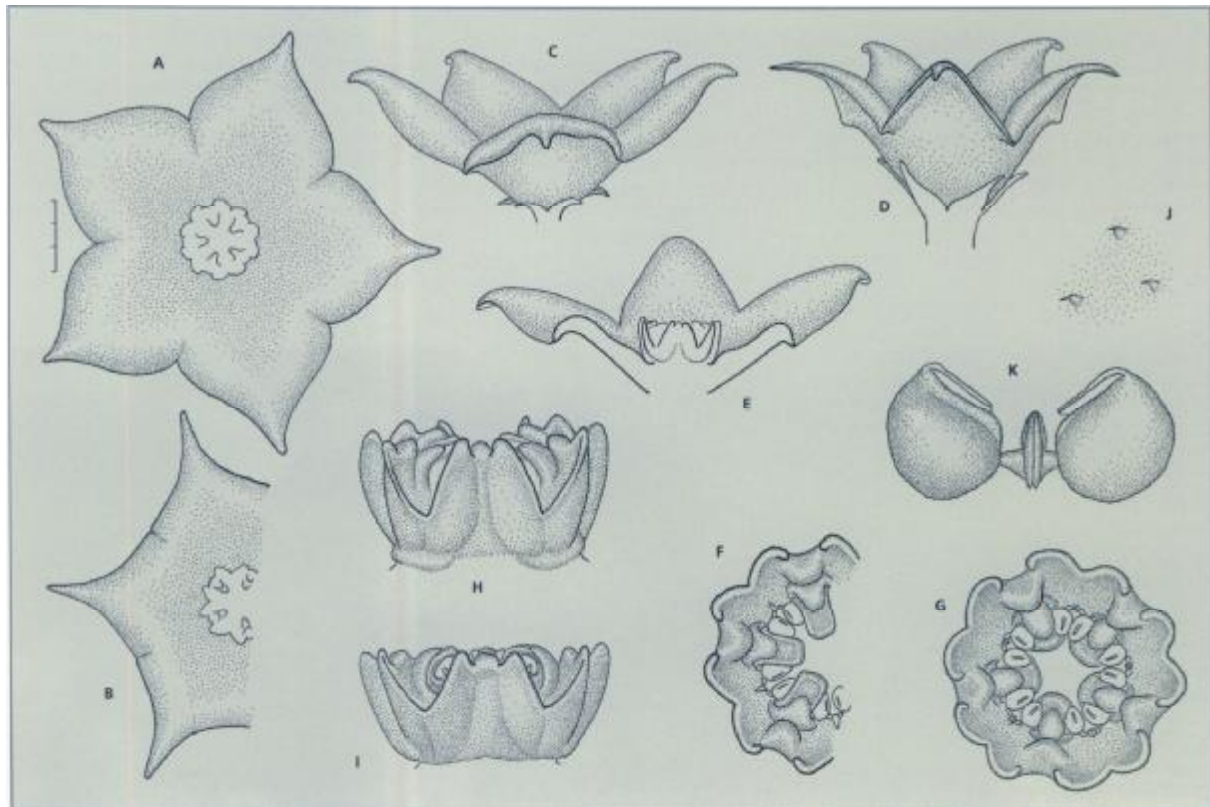


Fig. 4.14. *Hoodia officinalis* subsp. *deletaiana*. A, B, face view of flower. C, D, side view of flower. E, side view of dissected flower. F, G, face view of gynostegium. H, I, side view of gynostegium. J, papillae inside corolla; K, pollinarium. Scale bars: A-E, 3 mm (at A); F-I, 1 mm (at A); J, 0.5 mm (at A); K, 0.25 mm (at A). Drawn from: A, C, E, G, H, J, Bayer sub KG 553/77, Klinghardt Mountains, Namibia; B, D, F, I, K, Bayer 3858, Klinghardt Mountains, Namibia.



Fig. 4.15. *H. officinalis* subsp. *delaetiana*, S. Hammer, Klinghardt Mountains, Namibia, an unusually yellow-flowered plant.

Distribution and habitat

Hoodia officinalis subsp. *delaetiana* is known only in the south-western corner of Namibia, quite close to the coast. Here it occurs in the Klinghardt Mountains, which lie about 100 km south of Lüderitz, in the so-called *Sperrgebiet*. It is locally quite common and is the only member of *Hoodia* that is found there, with populations of *H. alstonii* to the north-east and south-east. The nearest populations of subsp. *officinalis* are some 80 km away to the north-east in the Huib-Hochland and out of the strictly winter-rainfall area where subsp. *delaetiana* occurs.

Plants grow in stony flats and on low, stony hills. In this area wind-blown sand fills up many of the crevices between the rocks and there is very little other vegetation.

Diagnostic features and relationships

In subsp. *delaetiana* the plant is generally a little more stoutly spiny and more robust than in subsp. *officinalis*. Specimens often form a shrub up to 200 mm tall (fig. 36 B), but may sometimes be found with almost completely prostrate stems. In addition, the flowers are larger (up to 20 mm across) with a broader and much flatter tube to the corolla. Inside they vary in colour from yellow to dark brownish yellow but are never the brownish pink that is often seen in subsp. *officinalis*. Although the inside of the corolla has been given as smooth this is not always true and it may have scattered papillae on the surface. These papillae are also tipped with a small apical bristle which is, however, not as long as that in subsp. *officinalis*. The two subspecies share an identical gynostegium.

History

Subsp. *delaetiana* was discovered by M. Kurt Dinter on 13 September 1922 (Dinter 1923: 50) and named by him for the Belgian dealer in succulents, F. de Laet. Curiously enough, Dinter gave the type the same collecting number as the type of *Strumaria phonolithica*, also from the same area, but both specimens are missing!

3. *Hoodia flava*

Hoodia flava (N.E.Br.) Plowes, *Asklepios* 56: 8 (1992).

Trichocaulon flavum N.E.Br., *J. Linn. Soc. Bot.* 17: 165, t.11, fig. 2-4 (1878).

Type: South Africa, Karoo, Bain (K).

Shrub with 3-many stems, up to 0.5 m tall and 0.3 m broad but mostly much smaller. Stems 75-300 mm long, (20-) 35-70 mm thick, erect, greyish to brownish green; tubercles fused below middle into 18-31 acute angles along stem, each tipped with a pale to dark brown weak spine 4-6 mm long. Inflorescences each with 1-3 flowers; pedicel 0.5-1.0 mm long, 0.5-1.0 mm thick; sepals 2.5-3.0 mm long, 1.0-1.5 mm broad at base, ovate-lanceolate, acuminate, adpressed to corolla. Corolla 10-15 mm diam., ± rotate, lobed to halfway down, inside greenish yellow sometimes with brown tips to lobes or wholly brown, minutely papillate (papillae rounded with fine apical bristle) to smooth; tube < 1 mm deep, united part of corolla flat to slightly saucer-shaped with distinct thickening around base of gynostegium which gives rise to tube; lobes 2.5-4.0 mm long, 3.5-5.0 mm broad at base, spreading, broadly ovate-deltate, acuminate. Corona 2-3 mm tall, 5-6 mm broad, slightly translucent yellow (occasionally faintly brownish translucent), glabrous, raised on short stipe; outer lobes 1.6-2.2 mm long, spreading, bifid below middle into dorsiventrally flattened linear obtuse lobules (those of adjacent lobes usually connivent); inner lobes 0.5-1.0 mm long, linear, obtuse, with narrow dorsal ridge near base joined to outer lobes.

Distribution and habitat

Hoodia flava is not quite as widely distributed as *H. officinalis*. It is recorded in southern Namibia from the eastern and southern flanks

of the Great Karas Mountains. In the Northern Cape it occurs just east of the winter-rainfall region in the quartz hills around Pofadder in Bushmanland but it is much more regularly encountered on the southern edge of Bushmanland from Calvinia to Camarvon, from where it extends southwards across the Great Karoo towards Prince Albert and Rietbron. It is quite plentiful in some localities between Calvinia, Britstown and Beaufort West, but becomes rare further south towards Prince Albert and Rietbron. It appears to be very rare between Pofadder and Vanwyksvlei, where there is a gap in the documented distribution.

Plants often grow on gentle, gravelly slopes or the summits of hills inside bushes. They have also been found several times in flat areas devoid of stones, growing well hidden inside shrubs. Specimens will often be found inside shrubs of the gregarious and spiny *Ruschia spinosa* and *R. divaricata* in western localities (especially between Williston and Fraserburg, as in fig. 4.22). They are also often associated with colonies of *Rhigozum trichotomum* further north and east, and from Beaufort West to Prince Albert and Rietbron they are mostly encountered inside shrubs of *R. obovatum* and again among the gregarious, spiny *Ruschia cradockensis*.

Diagnostic features and relationships

As with *H. officinalis*, *H. flava* is very variable in size and one may occasionally find a large plant up to 500 mm tall with stems 60-70 mm thick. Such a substantial plant forms a robust shrub within a bush or will even sometimes stand on its own in the open. However, most plants are

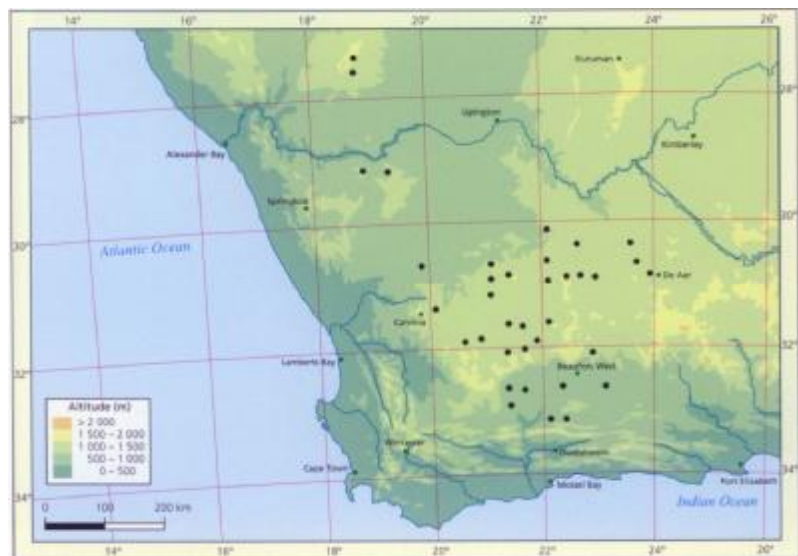


Fig. 4.16. Distribution of *Hoodia flava*.

HOODIA FLAVA

smaller and they will even be found flowering in the field at a height of 75 mm or less, which is probably achieved after two years from seed if conditions are favourable.

The flowers of *H. flava* are small and rarely exceed 12 mm in diameter. They are relatively flat, with broad and short, spreading lobes and inside they are usually greenish yellow with the

upper half of the lobes suffused with brown. Two localities found in Namibia have both yielded plants with entirely brown flowers (fig. 4.21) and others with the usual greenish yellow but sometimes even greenish yellow without the characteristic brownish tips to the lobes. This variability in colour has not been found in South Africa, despite many plants having been

observed in flower in many localities. In *H. flava* there is only a very slight annular thickening near the base of the corolla. This forms a tiny, steep tube in most flowers, but the fairly prominent stipe on which the gynostegium sits raises the corona beyond this tubelet. The inner surface of the corolla is covered with minute papillae which are not, however, readily seen

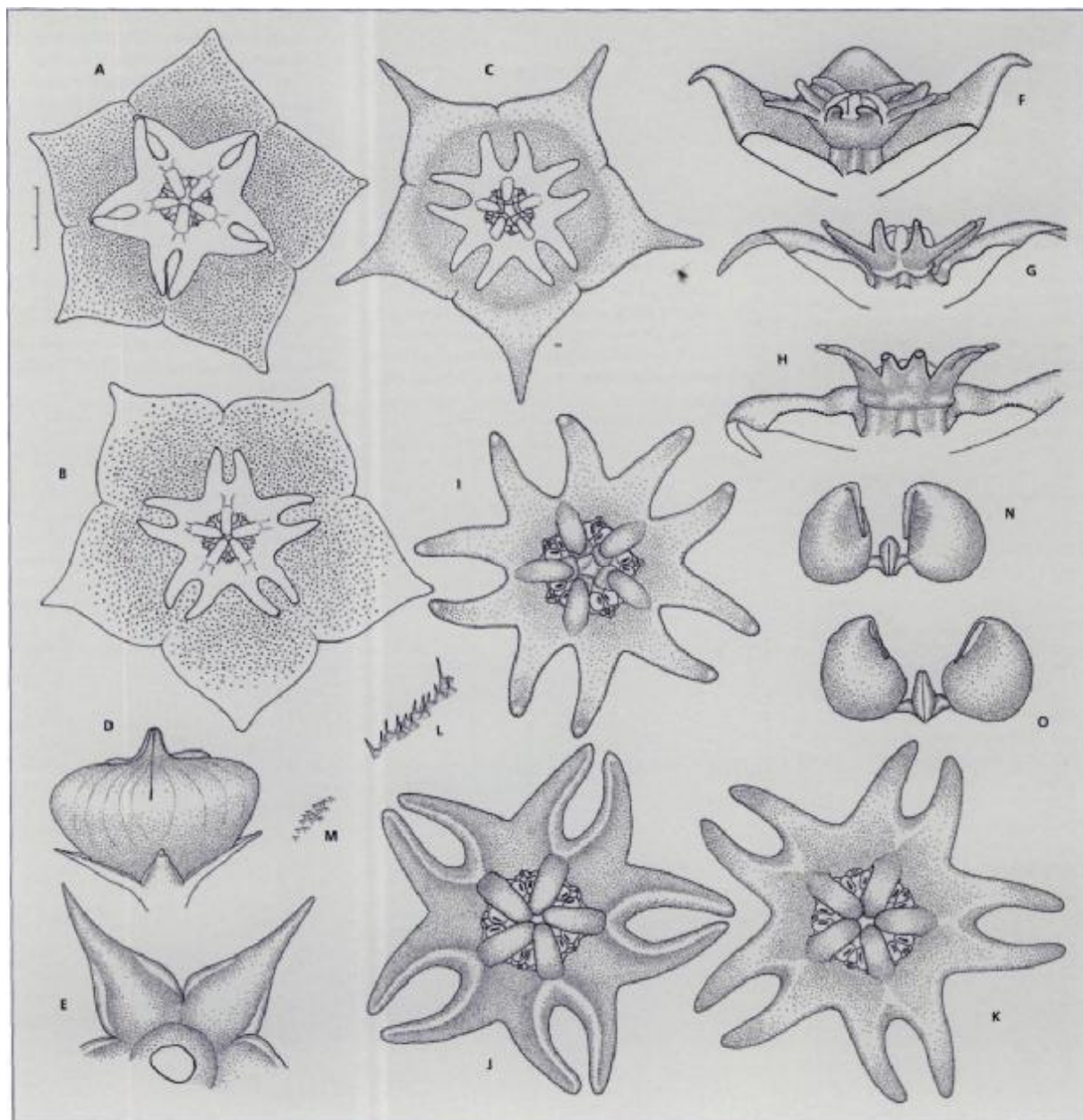


Fig. 4.17. *Hoodia flava*. A-C, face view of flower. D, bud. E, view from rear, of calyx. F-H, side view of dissected flower. I-K, face view of gynostegium. L, M, papillae inside corolla below base of lobes. N, O, pollinarium. Scale bars: A-D, F-H, 2 mm (at A); E, I-K, 1 mm (at A); L, M, 0.5 mm (at A); N, O, 0.25 mm (at A). Drawn from: A, E, F, J, M, PVB 1122, east of Calvinia; B, D, H, K, O, PVB 3050, Twyfelhoek, De Aar; C, G, I, L, PVB 3494, Great Karas Mountains, Namibia; N, PVB 1259, Spitzkop, Merweville.

without a microscope.

The corona is comparatively flat and, at 5-6 mm in diameter, is quite large relative to the size of the flower. The lobes are normally bright translucent yellow but in brown-flowered plants they are translucent yellow-white or slightly suffused with brown. The outer lobes are relatively obvious and mandible-like. They spread out widely above the surface of the corolla and are usually somewhat channeled below the guide-rails. The inner lobes are small but hide the anthers.

Hoodia flava differs from all others by its almost flat flower (occasionally campanulate from pressure exerted by surrounding tubercles and spines) with only very minute papillae on the inner surface and the widely spreading outer corona lobes. The structure of the corona is quite similar to that of *H. grandis* and *H. pilifera*. However, in these two the outer corona lobes rise up steeply and thus are far more deeply cupular around the gynostegium. In addition, the papillae on the inside of the corolla are much larger in *H. grandis* and *H. pilifera*. In the other yellow-flowered species, *H. alstonii*, the outer corona lobes are also much more erect and the flower is always campanulate. Furthermore, in *H. alstonii* it is completely devoid of papillae inside and the pollinia have an unusual shape that is not found elsewhere in *Hoodia*.

History

Hoodia flava was first recorded by Thomas C. Bain, who sent material from an undisclosed locality in the Karoo to N.E. Brown via Henry Barkly between 1870 and 1877. It was this material that N.E. Brown used chiefly to draw up his description of *Trichocaulon*.

This species has been exceptionally rarely recorded in Namibia. It appears that it was first observed there on 2 May 1913 by Kurt Dinter and Adolf Engler who collected a thorny *Trichocaulon* 'with insignificant flowers' at the mouth of the Us River gorge at the southern end of the Great Karas Mountains (Dinter 1921: 108). Dinter dubbed these plants '*T. karasmontanum*'. I have not located a specimen of this collection but it is probably *H. flava* rather than *H. officinalis*, which he knew well (Dinter 1914) and which does not appear to grow around the southern and eastern sides of these mountains. It was gathered again in May 1936 in Namibia by N.J.G. Smith (PRE records).



Fig. 4.18. *H. flava*, PVB 7549, north of Williston.



Fig. 4.19. *H. flava*, PVB 1122, east of Calvinia, in habitat, May 1998.



Fig. 4.20. *H. flava*, PVB 3743, 130 km south of Prieska. Here the flowers lack the typical, slightly brownish border and tips to the lobes.



Fig. 4.21. *H. flava*, PVB 3494, Great Karas Mountains, Namibia. Plants with brown flowers like this are only known from this area.



Fig. 4.22. *H. flava*, PVB 1122 east of Calvinia, a large specimen about 30 cm tall at the base of a shrub of *Ruschia divaricata*, May 1998.

HOODIA ALSTONII

4. *Hoodia alstonii*

Hoodia alstonii (N.E.Br.) Plowes, *Asklepios* 56: 7 (1992).

Trichocaulon alstonii N.E.Br., *Bull. Misc. Inform.* 1906: 166 (1906).

Type: South Africa, Cape, stony fields near Namies, 900 m, *Alston sub MacOwan* 2017 (K, holo.; SAM, iso.).

Many-stemmed often dense shrub up to 1 m tall and 0.5 m broad. *Stems* 0.1-1.0 m tall, 40-80 mm thick, erect, whitish grey-green; *tubercles* fused below middle into 20-22 obtuse angles along stem, each tipped by a stout sharp pale brown spine (6-) 8-10 mm long. *Inflorescences* mostly in upper parts of stem, each with 1-8 flowers arising in time from short stumpy peduncle (< 5 mm long); *pedicel* 1-2 (-4) mm long, 0.5-1.0 mm thick; *sepals* 2.0-2.5 mm long, $\pm$ 1 mm broad at base, ovate, acuminate. *Corolla* 10-18 mm diam, campanulate; outside pale greenish yellow to cream; inside bright yellow becoming whitish towards base, without papillae; *tube* 2-3 (-4) mm deep, broadly conical; *lobes* (4-) 6-8 mm long, 4-5 mm broad at base, spreading to ascending, ovate-deltate, acute, convex above from reflexed margins. *Corona* 2 mm tall, 2.5-3.0 mm broad, pale yellow, glabrous, raised on short stipe; *outer lobes* 1.0-1.5 mm long, erect, bifid at least to level of base of inner lobes into erect gradually tapering obtuse lobules; *inner lobes* $\pm$ 0.5 mm long, adpressed to backs of anthers and usually exceeding them, oblong, obtuse.

Distribution and habitat

Hoodia alstonii has an unusual distribution within the winter-rainfall region of southern Namibia and in the western parts of the Northern Cape. It occurs in three apparently discrete areas which are separated at their nearest points by some 150 km. The northernmost of these consists of several gravelly, quartz and schist hillsides in the Namib Desert from 30-50 km east of Lüderitz northwards to Uri Hauchab. Here plants are extremely common, for example on the Hahlenberg, roughly in the centre of this area, but are much rarer on other similar prominences nearby and the species may be more widely distributed in these parts than the records show. The other two areas where it occurs are along the lower reaches of the Orange River. The more extensive of these is in the mountainous country along the lower Orange River from Umdaus north of Steinkopf to the Obib Mountains, west of Sendelingsdrift. Here *H. alstonii* grows on both banks of the river (i.e. in Namibia and in South Africa) and is mainly found on schist slopes and outcrops but occasionally also on quartz ridges. The remaining area is in the flat-topped quartz mountains in the vicinity of Aggenys, Pella and Pofadder, where it seems to occur mainly on the summits of these ridges but in this case only on the south bank of the river i.e. in South Africa. This area falls outside the winter-rainfall region.

Hoodia alstonii inhabits remarkably arid

places. Specimens of any size are generally found fully in the open on rocky slopes or stony, flat areas. Several times plants have been seen rooted in almost impossibly narrow crevices in rock outcrops where they still manage to reach a considerable size (fig. 61). They are often very scattered but occasionally small, localised colonies may be encountered.

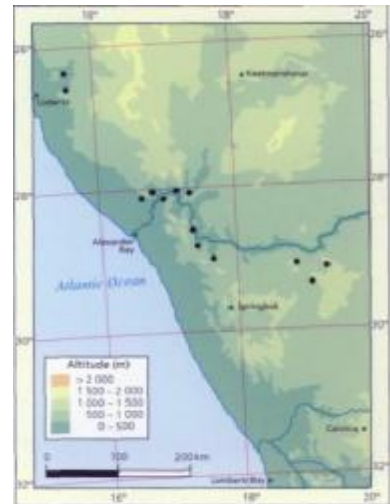


Fig. 4.23. Distribution of *Hoodia alstonii*.

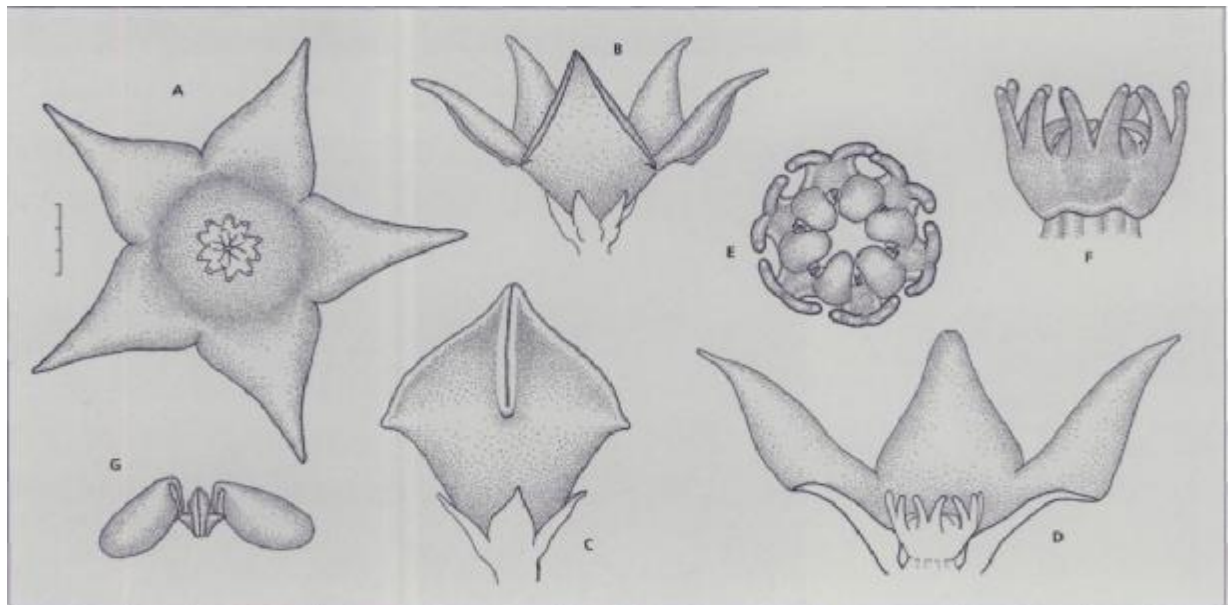


Fig. 4.24. *Hoodia alstonii*. A, face view of flower. B, side view of flower. C, bud. D, side view of dissected flower. E, face view of gynostegium. F, side view of gynostegium. G, pollinarium. Scale bars: A, B, 3 mm (at A); C, D, 2 mm (at A); E, F, 1 mm (at A); G, 0.25 mm (at A). Drawn from: A, M. Visagie, Hahlenberg, Namibia; rest, PVB 1327, Swartpoort, near Sendelingsdrift, Richtersveld.

Diagnostic features and relationships

Specimens of *H. alstonii* may reach a height of 1 m or slightly more and thus they are by far the tallest of the small-flowered species of *Hoodia*. Plants in the Pofadder district seem to be markedly smaller than further west, starting to flower when only 80 mm tall and rarely exceeding 300 mm in height. The stout stems are armed with extremely hard, sharp spines, much like those of *H. gordonii* and they are similarly difficult to handle. They have a whitish, grey-green colour which is also characteristic and unusual.

Flowers are produced in large numbers on the upper parts of the stems, arising on peduncular patches of which parts may eventually elongate to a few millimeters. Although the flowers are fairly small, they are bright yellow and consequently they may make quite a show and cover the top of the plant with yellow. Their beauty is combined with quite a strong, sweetish, fruity odour that is unusual in *Hoodia*.

The flowers of *H. alstonii* are peculiar for the thin texture of the corolla, which is also entirely without papillae on the inside. The corolla lobes are also narrower than in most of the Cape species and this is somewhat accentuated by the extent to which the margins are folded back. The lobes generally tend to be ascending and there is a shallow tube below them so that the flower has a campanulate shape. This tube becomes much steeper up against the lower part of the gynostegium, where it is also somewhat thickened.

The outer corona lobes are deeply divided into relatively slender lobules that ascend steeply around the gynostegium and very much restrict access to the guide-rails. The inner lobes are comparatively broad and hide the anthers completely and this also restricts access to the pollinaria. Consequently this species is much more difficult to pollinate by hand than any other in the genus. *Hoodia alstonii* is unique in the genus for the shape of the pollinium which is considerably broader than long, with the insertion-crest on the short side. Perhaps most surprising is the fact that, although plants of this species are generally so robust and substantial, they produce the smallest follicles in the genus. These are often only 30 mm long, with 50 to 60 seeds per pair.

History

Hoodia alstonii was discovered by Edward Garwood Alston (14 Jan. 1861 - 1 Dec. 1934) probably around 1890 in the Pofadder district. Born in Cape Town, Alston was a captain in the field intelligence department of the British Army during the Boer War. He also farmed for a while with his father at Vanwyksvlei. From 1912 until 1914 he was mayor of De Wetsdorp and from 1914 he lived in Ceres, where he became deputy mayor, after which he retired to Durban



Fig. 4.25. *H. alstonii*, PVB 7246, Stormberg, southern Namibia.



Fig. 4.26. *H. alstonii*, PVB 1327, Swartpoort, near Sendelingsdrift, Richtersveld.



Fig. 4.27. *H. alstonii*, among quartz rocks at Umdaus, south-eastern Richtersveld, September 1993 (photo: J.A. Retief).

(R.G. Alston, pers. comm. 2002).

Hoodia alstonii was first collected in Namibia only quite a bit later. Although Dinter spent a few days at Hahlenberg in 1922 (Dinter 1923: 32), he did not record *H. alstonii* on that

occasion, only collecting it for the first time there in January 1929 and in Kahanstal, south-east of Rosh Pinah, in December 1934. He called these plants *Trichocaulon halenbergense* but this name was never validly published.

HOODIA PILIFERA

5. *Hoodia pilifera*

Hoodia pilifera (Lf.) Plowes, *Asklepios* 56:10 (1992).

Stapelia pilifera L.f., *Suppl. Pl.* 171 (1781).

Piarranthus piliferus (L.f.) Sweet, *Hort. Brit.*, ed. 2: 359 (1830).

Trichocaulon piliferum (L.f.) N.E.Br., *J. Linn. Soc. Bot.* 17:164 (1878).

Type: South Africa, Cape, in Karoo beyond

Attaquas Kloof, Thunberg & Masson 6332 (UPS).

Few- to many-stemmed shrublet to large shrub up to 0.8 m tall and 2 m broad. Stems 0.1-0.8 m tall, 30-60 mm thick, erect, dark greyish green; tubercles fused below middle into 20-34 acute to obtuse angles along stem, each tipped with a stiff grey to brown spine 3-9 mm long. Inflorescences each with 1-3 evil smelling flowers opening successively; pedicel 0.5-1.5 mm long, 1.0-1.5 mm thick (flower nearly sessile); sepal 1.5-3.0 mm long, 1.0-1.5

mm broad at base, ovate-lanceolate, acuminate. Corolla 8-30 mm diam., rotate to campanulate; inside pinkish brown to dark purple-black, covered (except towards base of tube) with conical obtuse papillae each tipped with a spreading bristle; tube 2-4 mm deep, 3.5-5.0 mm broad at mouth, cupular, usually with raised thickened annulus in corolla forming mouth; lobes 3.5-9.0 mm long, 3-9 mm broad at base, ascending to spreading, broadly ovate-delate, acuminate, margins only slightly folded back. Corona

2-4 mm tall, 3-6 mm broad, glabrous, dark purple-black becoming reddish towards base, raised on very short stipe; outer lobes 1.5-4.0 mm long, erect, bifid to at least half their length into spreading and widely diverging dorsiventrally flattened lanceolate obtuse lobules, laterally fused in lower half to bases of inner lobes to form deep bay around guide-rails; inner lobes 0.5-1.5 mm long, linear, obtuse, from half as long as to equalling anthers (rarely connivent and rising up in centre).

Key to the subspecies of *H. pilifera*

Corolla (13-) 20-30 mm diam., inside dark purple-black, lobes spreading and

usually adpressed to stem, plants from east of 22°E

5b. subsp. *annulata*

Corolla 16-20 mm diam., inside dark purple-black to pinkish brown, lobes erect

to spreading, plants from west of 22°E

5a. subsp. *pilifera*

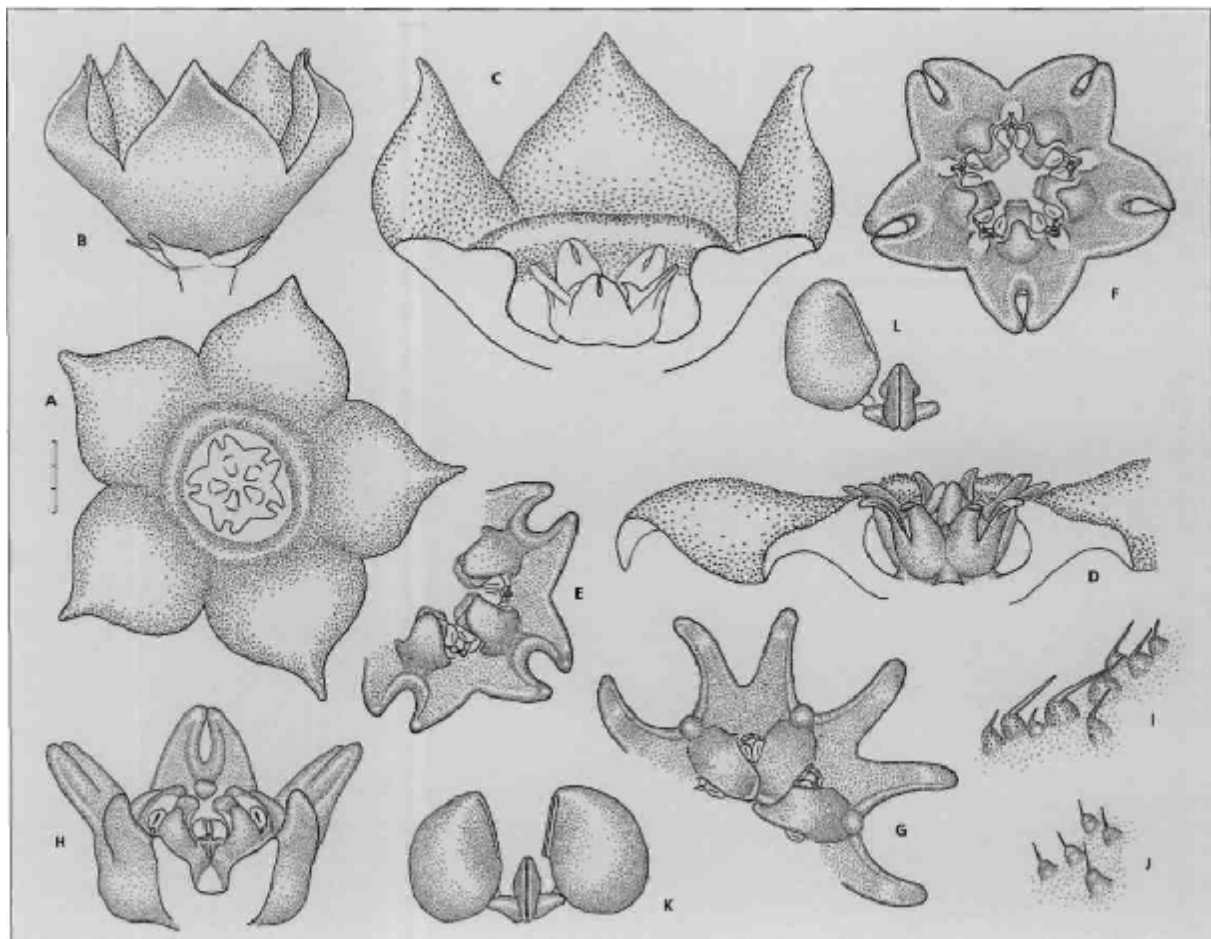


Fig. 428. *Hoodia pilifera* subsp. *pilifera*. A, face view of flower, flattened out. B, side view of flower showing usual shape. C, D, side view of dissected flower. E-G, face view of gynostegium (or part of it). H, side view of gynostegium with one outer corona lobe removed. I, J, papillae inside corolla. K, L, pollinarium. Scale bars: A, B, 3 mm (at A); C, D, 2 mm (at A); E-H, 1 mm (at A); I, J, 0.5 mm (at A); K, L, 0.25 mm (at A). Drawn from: A, E, H, J, K, *Bayer 2449*, Witteberg; B, C, F, *PVB 924*, north-east of Montagu; D, G, I, L, *Kratz*, south-west of Laingsburg.

5a. *Hoodia pilifera* subsp. *pilifera*

Few- to many-stemmed shrublet to 800 mm tall. Stems with 21-34 acute to obtuse angles, spines 5-9 mm long. Corolla 16-20 mm diam., usually somewhat campanulate with lobes only slightly spreading and often with slight annulus; outside reddish green; inside dark purple-black to pinkish brown; tube 2.0-2.5 mm deep, with corolla much thickened into annulus and thereby giving rise to often rather constricted sub-pentagonal mouth 4-5 mm diam.; lobes 4-6 mm long, 6-7 mm broad at base, ascending to spreading. Corona 2-3 mm tall, 4-5 mm broad; outer lobes bifid to well below middle into spreading to sub-erect diverging dorsiventrally flattened lobules 1-2 mm long; inner lobes 0.5-1.0 mm long.

Distribution and habitat

Hoodia pilifera subsp. *pilifera* is confined to the south-western corner of the region over which the genus is distributed. It is found in the Little Karoo from Montagu to west of Uniondale and in the southern edge of the Great Karoo from Matjiesfontein eastwards to Laingsburg and Gamka Poort. East of Gamka Poort towards Prince Albert it disappears on the northern side of the Swartberg but reappears east of Klaarstroom. Records are few and sparse and it appears to be quite rare, probably due to the degradation of habitat by overgrazing and the eating of plants by humans.

Plants are usually found inside bushes on steep shale slopes or near the foot of sandstone mountains. They usually grow on the hotter northern to eastern aspect but I have seen the occasional specimen in flat areas and even on cooler south slopes.

Diagnostic features and relationships

At the western end of the Little Karoo, *H. pilifera* subsp. *pilifera* is quite distinctive. It has relatively small flowers which are very dark purple-brown or practically black, becoming somewhat paler around and inside the tube. The flowers usually do not open fully and are kept partially closed by pressure from the surrounding tubercles on the stem. They have

a quite prominently thickened annulus which projects inwards to form an abrupt mouth to the cupular corolla tube. This tube more or less completely contains the gynostegium. Most of the inside of the flower (except inside the tube) is covered with fairly obvious papillae. The corona is usually as dark as the corolla and the deeply bifid outer lobes are fused towards the base into a cup around the gynostegium. The inner lobes are usually shorter than the anthers but are closely adpressed to their backs. Plants with identical flowers to these are found in the dry valleys east of Klaarstroom (e.g. fig. 4.31) and around Oudtshoorn. The flowers in subsp. *pilifera* emit an excrement-like odour.

Within the Witteberg, from west of Laingsburg to Gamka Poort, specimens produce larger flowers which usually open fully and are a pinkish brown colour. The corona is still practically black, often with long inner lobes which touch in the centre and may rise up in a small column. These flowers have a broad, flat, united portion to the corolla and there is a considerable annulus forming the mouth of the tube. The broad corolla and the long inner corona lobes suggest that these plants could be referred to subsp. *annulata* but geographically they fit better into subsp. *pilifera*. The well-developed annulus and the blackish corona ensure that these specimens cannot be confused with *H. grandis*.

History

Subsp. *pilifera* was discovered by Thunberg and Masson in January 1774 in the vicinity of the present-day Oudtshoorn and Thunberg's specimen from this collection was seen by the son of Linnaeus and described by him as *Stapelia pilifera*. For some reason Masson mentioned in his *Stapeliae Novae* that it came from the Karoo below the Roggeveld but this must be an error.

Two records are known from far outside this area: Huber (1967) cited a specimen of Range from the Arasabkuppe near Lüderitz in Namibia and Steenkamp & Vahrmeyer recorded it from Botswana (without exact locality, PRE). I have not been able to locate Range's specimen but these are both certainly errors.



Fig. 4.29. *H. pilifera* subsp. *pilifera*, Heunis 7567, east of Montagu.



Fig. 4.30. *H. pilifera* subsp. *pilifera*, PVB 4201, south-east of Laingsburg on the road to Seweweekspoort. Flowers in this area are much paler than is typical for subsp. *pilifera*.



Fig. 4.31. *H. pilifera* subsp. *pilifera*, PVB 4961, east of Klaarstroom.

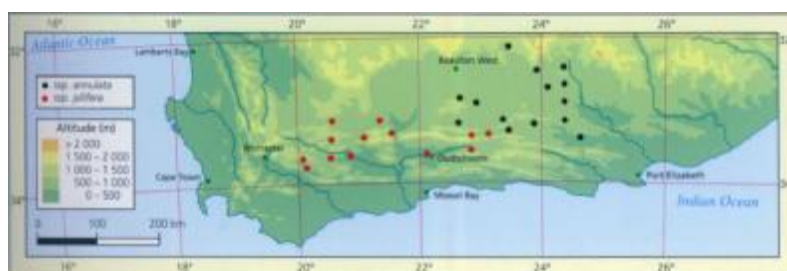


Fig. 4.32. Distribution of *Hoodia pilifera*.

5b. *Hoodia pilifera* subsp. *annulata*

Hoodia pilifera subsp. *annulata* (N.E.Br.) Bruyns, *Bot. Jahrb. Syst.* 115: 235 (1993).

Trichocaulon annulatum N.E.Br., *Fl. Cap.* 4 (1): 889 (1909).

Hoodia annulata (N.E.Br.) Plowes, *Asklepios* 56: 8 (1992).

Type: South Africa, Klipplaat, Lee sub N.S. Pillans 1351 (BOL).

Large many-stemmed shrub up to 0.5 m tall and 2 m broad. Stems with 20-22 (-30) angles, spines 3-5 (-6) mm long. Corolla (15-) 20-30 mm diam., rotate, with prominent central annulus; outside reddish purple to greenish towards base; inside dark purple-black; tube 3-4 mm deep, with corolla much thickened into erect annulus around mouth; lobes 5-7 mm long, 8-9 mm broad at base, spreading and usually adpressed to stem. Corona 4 mm tall, 5-6 mm broad; outer lobes bifid to near middle into widely spreading lobules 2.0-2.5 mm long; inner lobes $\pm$ 1 mm long.

Distribution and habitat

Hoodia pilifera subsp. *annulata* is found on the Great Karoo from Aberdeen and Graaff-Reinet southwards to Rietbron and eastwards to Willowmore, Klipplaat and Steytlerville.

Subsp. *annulata* mostly grows in flat areas between low hills in slightly gravelly ground. Only rarely has it been seen to grow on the slopes of hills. Plants are often very scattered with several hundred meters or more from one large plant to the next, but occasionally quite substantial colonies occur. One east of Willowmore was found to contain more than 50 large plants. The areas where it occurs are mostly covered with short *Pentzia* bushes (*Euphorbia ferox* is also often present) and there are few other shrubs exceeding 300 mm in height (except for some large forms of *Euphorbia polygona* in some places near Willowmore). Consequently, specimens of subsp. *annulata* are often the largest plants in the area and are then usually visible from a considerable distance.

Diagnostic features and relationships

Specimens of subsp. *annulata* may become enormous (fig. 4.35). Although the stems are rarely taller than 400 mm, they branch extensively from the base to form a low shrub. This may exceed 2 m in diameter and then consists of hundreds of stems. These large shrubs reach a considerable age and farmers in the area speak of individual massive specimens that they have known for 30-40 years.

Subsp. *annulata* has dark, purple-black flowers which open out fully against the stems, despite the extremely short pedicels. In this case the corolla tube is sufficiently long that the lobes are able to spread out beyond the tubercles and spines. The flowers are usually 20-30 mm in diameter but, as usual, this is subject to much variation and they may be as small as 15 mm diameter. They also have by far the most prominent annulus in the genus. Pressure from the surrounding tubercles often

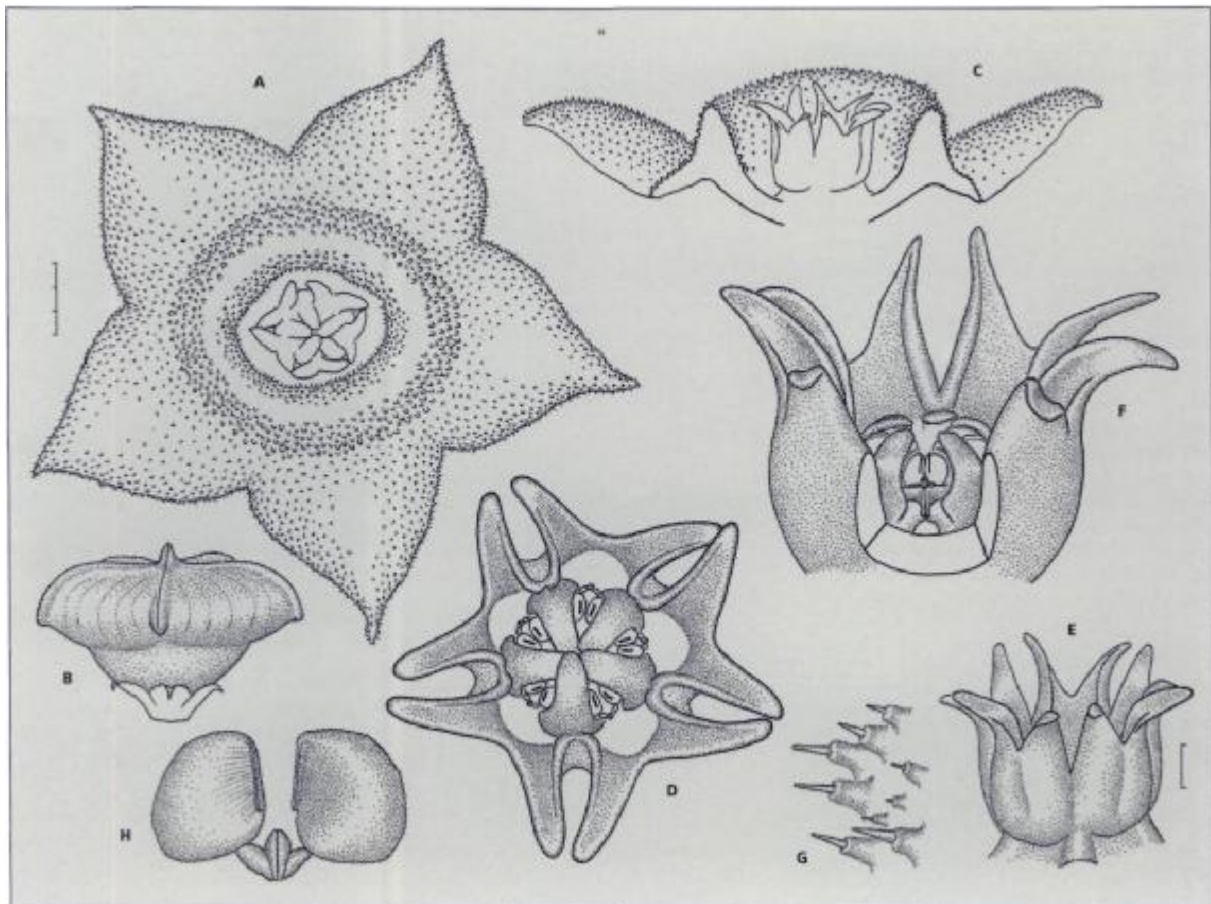


Fig. 4.33. *Hoodia pilifera* subsp. *annulata*. A, face view of flower. B, bud. C, side view of dissected flower. D, face view of gynostegium. E, side view of gynostegium. F, side view of gynostegium with one outer corona lobe removed. G, papillae inside corolla on annulus. H, pollinarium. Scale bars: A-C, 3 mm (at A); D, F, 1 mm (at A); E, 1 mm; G, 0.5 mm (at A); H, 0.25 mm (at A). Drawn from: B, Heunis, Abelshoek, Steytlerville; rest, Bayer sub KG 142/72, Constantia, Willowmore.

distorts the annulus and the shape of the tube. Nevertheless, the annulus forms a more or less elliptical mouth which projects straight out of the surface of the corolla to form a small tube containing the gynostegium. The inside of the corolla (including the annulus) is covered densely with papillae which are clearly visible to the naked eye. Like most dark-flowered stapeliads, the flowers emit an unpleasant, foetid, excrement-like odour.

The outer corona usually rises steeply and forms a cup around the anthers with ascending, then spreading, channeled lobes.

This subspecies differs mainly from subsp. *pilifera* in the habit (growing in flats, which is rare for subsp. *pilifera*, and forming huge clumps in the open) and in the much larger flowers: the corolla is generally larger and the corona is also larger, with a more prominent and deeper cup formed by the more erect outer lobes. However, pale-flowered plants of subsp. *pilifera* from around Laingsburg begin to approach subsp. *annulata* in the size of the flowers and it is only the small-flowered forms of subsp. *pilifera* from the west around Montagu and around Oudtshoorn that are clearly and easily separable from subsp. *annulata*.

History

Subsp. *annulata* was discovered by H. Lee, a farmer in the Klipplaat area, who collected it in 1908. He brought material to N.S. Pillans at the Bolus Herbarium and from there it was sent to N.E. Brown, who described it shortly afterwards.



Fig. 4.34. *H. pilifera* subsp. *annulata*, PVB 6313, north-west of Willowmore, in habitat, July 1995.



Fig. 4.35. *H. pilifera* subsp. *annulata*, PVB 6313, north-west of Willowmore. This plant was about 2 m in diameter and another large one can be seen in the background on the left, July 1995.



Fig. 4.36. *H. pilifera* subsp. *annulata*, PVB 4963, south-east of Willowmore.



Fig. 4.37. *H. pilifera* subsp. *annulata*, PVB 6313, north-west of Willowmore.

HOODIA GRANDIS

6. *Hoodia grandis*

Hoodia grandis (N.E.Br.) Plowes, *Asklepios* 56: 9 (1992).

Trichocaulon grande N.E.Br., R Cap. 4 (1): 892 (1909).
Type: South Africa, after descent on northern slopes of Klein Swartberg on Ladismith-Laingsburg road, N.S. Pillans 668 (K, holo., BOL, iso.).

Trichocaulon pillansii N.E.Br., Gard. Chron. Ser. 3, 35: 242 (1904).

Hoodia pilifera subsp. *pillansii* (N.E.Br.) Bruyns, Bot. Jahrb. Syst. 115: 238 (1993).

Hoodia coleorum Plowes, *Asklepios* 56: 8 (1992), as '*H. cole*'.

Type: South Africa, Cape, south-east of Sout Kloof farmhouse, 1902, N.S. Pillans 9 (K, holo., BOL, iso.).

Trichocaulon pillansii var. *major* N.E.Br., Gard. Chron. Ser. 3, 35: 242 (1904).

Type: south-east of Sout Kloof farmhouse, N.S. Pillans 160 (BOL).

Few too many-stemmed shrub to 0.3 (-0.6) m tall and 0.5 m broad. Stems 0.1-0.8 m tall, 30-60 mm thick, erect, dark greyish green; tubercles fused below middle into 25-34 acute to obtuse angles along stem, each tipped with a stiff grey to brown spine 5-6 mm long. Inflorescences each with 1-3 flowers opening successively; pedicel 0.5-1.5

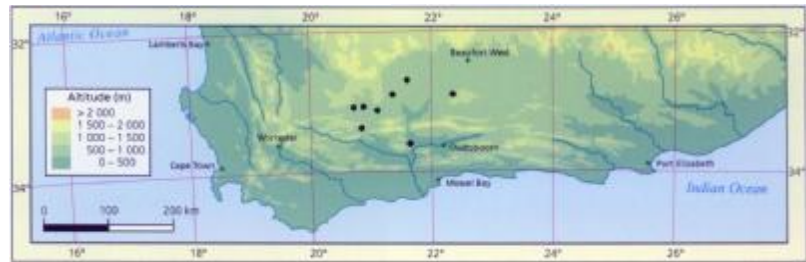


Fig. 4.38. Distribution of *Hoodia grandis*.

mm long, 1.0-1.5 mm thick (flower nearly sessile); sepals 1.5-3.0 mm long, 1.0-1.5 mm broad at base, ovate-lanceolate, acuminate. Corolla 8-20 mm diam., campanulate; outside pale pinkish green becoming darker towards tips of lobes; inside pale yellow to greenish yellow to pinkish, covered (except towards base of tube) with conical obtuse papillae each tipped with a tiny spreading bristle; tube 2-3 mm deep, 3.5-5.0 mm broad at mouth, cupular, with corolla slightly thickened at mouth and sometimes forming slight annulus; lobes 3.5-9.0 mm long, 3-7 mm broad at base, spreading, ovate-deltate, acuminate, often with margins strongly folded back. Corona 2 mm tall, 3-4 mm broad, glabrous, yellow (usually brighter than corolla), raised on very short stipe; outer lobes 1.5-4.0

mm long, erect, bifid to slightly below middle into ± erect dorsiventrally flattened lanceolate obtuse lobules up to 1 mm long, laterally fused in lower half to bases of inner lobes to form deep bay around guide-rails; inner lobes 0.5-1.0 (-1.5) mm long, linear, obtuse, from half as long as to equalling anthers.

Distribution and habitat

Hoodia grandis occurs east of the Roggeveld Plateau from just south of Merweville to the northern slopes of the high tillite ridge of the Dwyka series running parallel to and north of the Witteberge from Matjiesfontein

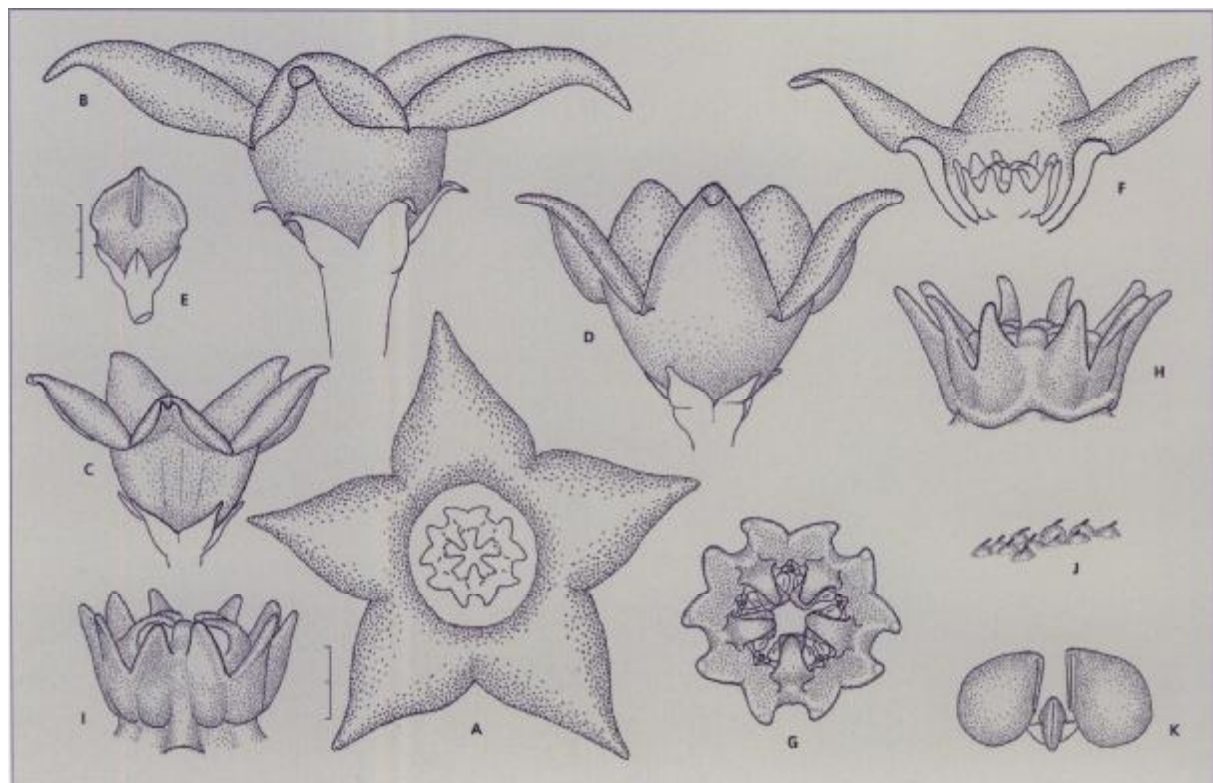


Fig. 4.39. *Hoodia grandis*. A, face view of flower. B-D, side view of flower. E, bud. F, side view of dissected flower. G, face view of gynostegium. H, I, side view of gynostegium. J, papillae inside corolla on lobe, apical bristles pointing towards tip of lobe. K, pollinarium. Scale bars: A-D, F, 2 mm (at A); E, 3 mm; G-I, 1 mm (at A); J, 0.5 mm (at A); K, 0.25 mm (at A). Drawn from: A, D, F, G, I, PVB 3804, north of Laingsburg; B, H, PVB 1260, near Merweville; C, E, J, PVB 3149, south-east of Kruidfontein Siding.

to Laingsburg. Outliers exist south of the Witteberge to the west of the Rooinek Pass and another prolific isolated population exists south-east of Kruidfontein Siding in the Great Karoo. This species also occurs in another isolated area in the Little Karoo, namely along the arid lower northern slopes of the Rooiberg, near Calitzdorp.

The distribution of *H. grandis* interlinks partially with that of *H. flava*, which is also found south of Merweville and which also occurs in several widely scattered locations east and south of Kruidfontein. It is also found close to areas where *H. pilifera* occurs.

Hoodia grandis is usually found on gentle to steep, stony slopes among bushes.

Diagnostic features and relationships

In *H. grandis* large plants up to 0.5 m in diameter have been seen and individual stems may reach a length of 0.6 m (though 0.3 m is more usual), so specimens may form quite substantial shrubs.

Hoodia grandis is usually easily recognised and distinctive, especially in the northern part of its range, southwards to the Soutkloof area north of Laingsburg, in the populations south-east of Kruidfontein Siding and on the Little Karoo near Calitzdorp. The flowers are usually fairly small, at between 8 and 12 mm in diameter. Inside they are pale yellow with a slight suffusion of pink along the margins of the lobes towards their tips. However, even in this area they may be up to 20 mm in diameter, so the size alone is not reliable for distinguishing it from *H. pilifera*. The corolla lobes are relatively narrow and the margins are recurved, giving them a convex shape. The corolla tube is fairly deep and cupular but there is usually no thickening around its mouth (i.e. no annulus is present). The bright yellow corona (which is a slightly different yellow to that of the corolla) has erect and scarcely diverging outer lobes. The flowers emit a striking odour that is



Fig. 4.42. *H. grandis*, west of Rooinek Pass. Some very unusually-coloured plants have been seen in this area. This, figs. 4.40 and 4.41, are all of plants collected on the same farm and grown in Laingsburg. All of them have a slight annulus around the mouth of the corolla tube.



Fig. 4.40. *H. grandis*, west of Rooinek Pass.



Fig. 4.41. *H. grandis*, west of Rooinek Pass.

reminiscent of fish in some cases and of socks that badly need a wash in others.

West of the Rooinek Pass, *H. grandis* shows considerable variability. These plants are cut off from the main body of the distribution of *H. grandis* by populations with pinkish brown flowers around Laingsburg which are preferable to (and discussed under) *H. pilifera* subsp. *pilifera*. In this area the flowers may be somewhat larger than is usual for *H. grandis*. The colour of the flowers in these plants ranges from yellow to greenish brown and through yellowish pink to quite bright pink. The flowers also may have more broadly deltate corolla lobes which are less convex and there may be a slight thickening around the mouth of the corolla tube, giving rise to faint traces of an annulus. The corona is usually pale yellow and has spreading-erect outer lobes which scarcely diverge, as is typical for *H. grandis* over the rest of its range. It is possible that some of the more darkly coloured flowers that are found in *H. grandis* here are a consequence of hybridisation with *H. pilifera* subsp. *pilifera*.

History

The plants described as *Trichocaulon pillansii* were discovered in 1902 by N.S. Pillans at Soutkloof, which lies to the north of Laingsburg. In November of the same year he collected the var. *major* on the same farm. In November 1904, Pillans also discovered the material which N.E. Brown described as *Trichocaulon grande*. According to Brown (1907-9), the stems in *T. grande* were the tallest that were then known in the genus and this is where the epithet '*grande*' came from. In my previous account (Bruyns 1993), I treated this taxon as a subspecies of *H. pilifera* (as subsp. *pillansii*). However, I have now re-collected material of *H. grandis* around Calitzdorp (where an expedition from Kirstenbosch first located it in 1949), verifying without doubt that it occurs in this area. The complex distribution of this species (closely interlinked with that of *H. pilifera*) as well as the various morphological differences between the two, suggests that one is dealing here with a taxon that is distinct from *H. pilifera*.



Fig. 4.43. *H. grandis*, PVB 3149, south-east of Kruidfontein Siding. Small-flowered plants such as this are typical of this species to the north and east of Laingsburg and near Calitzdorp.

HOODIA RUSCHII

7. *Hoodia ruschii*

Hoodia ruschii Dinter, Feddes Repert. Spec. Nov. Regni Veg. 30:192 (1932).

Type: Namibia, Tiras Mountains, E.F.T. Rusch sub. Dinter 7976 (BOL, holo.; B, G, PRE, S, Z, iso.).

Many-stemmed shrub to 0.5 m tall and 0.5 m broad. Stems 0.1–0.5 m long, 40–60 mm thick, erect, brownish to grey-green; tubercles fused below middle into 22–28 angles along stem, each bearing a stiff spine 6–8 mm long. Inflorescences mainly in upper half of stem, each with 4–10 extremely foul-smelling flowers, often several opening simultaneously on each knob-like persistent peduncle; pedicel 2–4 mm long, 2 mm thick; sepals 2–4 mm long, 1–2 mm broad at base, lanceolate, acute. Corolla 20–40 mm diam., broadly campanulate; outside pale green to reddish towards base; inside red-brown, covered with conical obtuse papillae each tipped with a slender spreading bristle; tube 6–8 mm long, 8–10 mm broad at mouth, broadly conical becoming steep-sided in lower half, with corolla slightly thickened around gynostegium and touching sides of gynostegium; lobes 8–14 mm long, 9–14 mm broad at base, spreading with slightly recurved tips, ovate-deltate, acuminate, convex with margins distinctly folded back. Corona ± 1 mm tall, 2.0–2.2 mm broad, dark purple-black, glabrous, raised on short stipe; outer lobes ± 0.5 mm long, erect, bifid nearly right to base into erect obtuse lobules, laterally fused for whole length to base of inner lobes and not exceeding them; inner lobes deltoid, obtuse, $\pm$ half as long as anthers, with narrow dorsal ridge near base joined to outer lobes.

Distribution and habitat

Hoodia ruschii is known only from the eastern flank of the Tiras Mountains. It was also said to grow on Uri Hauchab, in the Namib Desert (Albers & Meve 2001) but this is a misidentification and should refer to *H. alstonii*.

In the Tiras Mountains *H. ruschii* grows on steep, granitic slopes among rocks and small bushes. Plants are not uncommon but are of rather scattered occurrence.

Diagnostic features and relationships

Specimens of *H. ruschii* may reach a diameter of 0.5 m and more or less the same in height. The stems are stout and densely covered with sharp, hard spines. In the field they assume a brownish colouring but they are usually a paler grey-green in cultivation.

Hoodia ruschii is remarkably floriferous and the upper parts of the stems can be covered with flowers if the plant is healthy, as in fig. 1151 of White & Sloane (1937). Flowering seems, in cultivation at least to continue for most of the summer months. The flowers arise from relatively large 'peduncular patches', which have a complicated organisation and there are often several flowers open simultaneously on each patch. In this species the flowers are

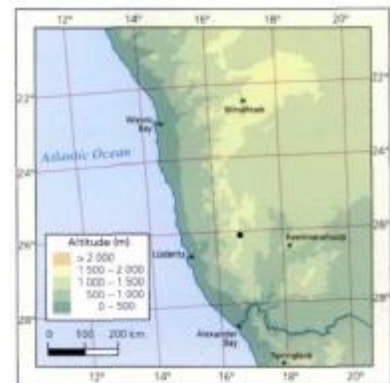


Fig. 4.44. Distribution of *Hoodia ruschii*.

relatively large for this section and usually at least 25 mm in diameter. They are funnel-shaped with relatively narrow lobes occupying about the same proportion of the diameter as the tube. The tube consists of a broad, more gently sloping part below the lobes which often becomes much steeper in the lower half and is distinctly thickened around the gynostegium. So, although there is no clear 'annulus' as in *H. parviflora*, the corolla here is similarly constructed. On the inside the flowers are

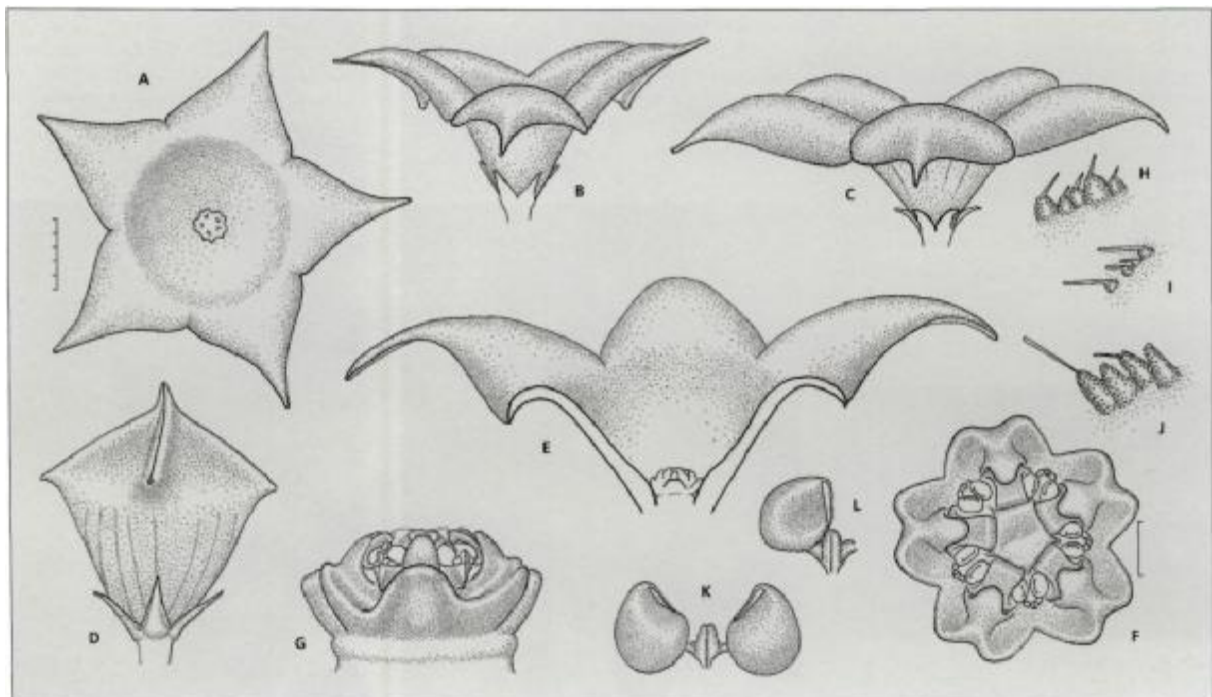


Fig. 4.45. *Hoodia ruschii*. A, face view of flower. B, C, side view of flower. D, bud. E, side view of dissected flower. F, face view of gynostegium. G, side view of gynostegium. H–J, papillae inside corolla with apical hairs directed towards apex of lobes: H, J, from sinuses of lobes; I, in base of tube. K, L, pollinarium. Scale bars: A–C, 5 mm (at A); D, E, 3 mm (at A); F, G, 0.5 mm (at F); H–J, 0.5 mm (at A); K, L, 0.25 mm (at A). Drawn from: PVB 1475, Tiras Mountains, Namibia.

deep red-brown and are densely covered with papillae, each with an apical bristle pointing towards the tips of the lobes. The apical bristle increases in length and the papilla becomes smaller towards the base of the tube and there the bristle is often longer than the papilla itself. The flowers emit a dreadful and extremely strong, excrement-like smell so that a single flower can be smelt readily from 30 cm away when it is placed under the microscope for drawing.

The gynostegium, which is nearly black, is remarkably small for the size of the flower. It consists of outer lobes which are deeply incised opposite the guide-rails, forming there only a shallow platform, with more significant lobules behind and fused to the inner lobes which are themselves quite short.

Hoodia ruschii is particularly closely allied to *H. triebneri* with which it shares the relatively densely flowered inflorescences, similar shape, colour and texture of the flowers and similar gynostegium. Despite their closeness, *H. ruschii* and *H. triebneri* are readily distinguished: in *H. ruschii* the stems are 40-60 mm thick with 22-28 angles, in *H. triebneri* 25-40 mm thick with 12-14 (-16) angles; in *H. ruschii* the flowers are red-brown, 20-40 mm across, with relatively large papillae, in *H. triebneri* they are blackish, 11-15 mm in diameter, with smaller papillae.

History

Hoodia ruschii was discovered somewhere in the Tiras Mountains by Ernst E.T. Rusch in 1931. It is very poorly known and, until recently, Rusch's collection was the only record that had been made of it.

Dinter described this species as a *Hoodia* and thought that it was related to *H. dregei* on account of the relatively small flowers. However, as White & Sloane (1937) pointed out, it is not closely allied to any of the erstwhile species of *Hoodia* but has its real affinities amongst the species formerly in *Trichocaulon*. In particular, it lacks the short and broad lobes with apical tail that is typical of all the species formerly included in *Hoodia*.



Fig. 4.46. *H. ruschii*, PVB 1475, Tiras Mountains, Namibia.



Fig. 4.47. *H. ruschii*, PVB 1475, Tiras Mountains, Namibia.

8. Hoodia triebneri

Hoodia triebneri (Nel) Bruyns, S. African J. Bot. 59: 342 (1993), non Schuldt (1933), nom. nud.
Trichocaulon triebneri Nel, Kakteenkunde 1935:117 (1935).

Hoodia foetida Plowes, Asklepios 56: 9 (1992).

Type: Namibia, near Okandu, 120 km east of Swakopmund, W. Triebner sub SUG 6020 (BOL).

Shrub up to 0.3 m tall and 0.5 m broad, with 10-30 stems. Stems 0.1-0.3 m long, 25-40 mm thick, erect; tubercles fused below middle into 12-14 (-16) angles, each tipped with a pale hard spine 5-6 mm long. Inflorescences mainly in upper part of stem, each with 6-12 extremely foul-smelling flowers, often several opening simultaneously on each eventually knob-like persistent peduncle; pedicel 3-4 mm long, ± 1 mm thick; sepals 2.2-2.5 mm long, ± 1 mm broad at base, ovate-acuminate. Corolla 11-15 mm diam, campanulate; outside reddish green; inside blackish red-purple (paler in base of tube), covered with conical obtuse papillae each tipped with a spreading bristle; tube 3.5-4.0 mm long, conical, with corolla somewhat thickened around gynostegium and touching sides of it; lobes 3.0-4.5 mm long, 4-5 mm broad at base, spreading, ovate-deltate, acuminate, sometimes with fine erect tip. Corona ± 1 mm tall, 2.0-2.2 mm broad, dark purple-black, glabrous, raised on short stipe; outer lobes ± 0.5 mm long, erect, bifid nearly right to base into erect obtuse lobules, laterally fused for whole length to base of inner lobes and not exceeding them; inner lobes deltoid, obtuse, $\pm$ half as long as anthers, with narrow dorsal ridge near base joined to outer lobes.

Distribution and habitat

Hoodia triebneri occurs only in Namibia along the Swakop River from west of Okahandja to near Otjimbingwe and Karibib.

Plants grow in gravelly flats around the bases of low ridges among scattered trees of *Acacia*.

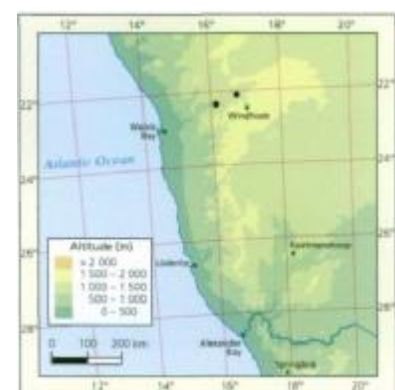


Fig. 4.48. Distribution of *Hoodia triebneri*.

HOODIA TRIEBNERI

Diagnostic features and relationships

Hoodia triebneri is a most unusual species. Plants form dense clumps of stems and are usually slightly broader than tall. The stems are erect and relatively slender, bearing strong spines on the tubercles which are arranged into 12 to 14 angles. They could easily, therefore, be mistaken for specimens of *H. gordonii*.

The appearance of flowers, however, immediately dispels any confusion. *Hoodia triebneri* is the first of the small-flowered species from the summer-rainfall areas to flower and in cultivation large numbers of flowers are usually produced for about five weeks in October and November. They arise in dense clusters and in each cluster several of the flowers open simulta-

neously. These clusters of flowers develop from flat 'peduncular patches' which are organised in a more complicated manner than in any other *Hoodia* except *H. ruschii*.

The flowers are small and nearly black, with short lobes spreading around the mouth of a funnel-shaped tube. On the inside the whole surface is densely covered with papillae, each with an apical bristle. As is often the case with very darkly coloured flowers, these are exceedingly foul-smelling. Near the base of the tube the walls are somewhat thicker around the corona so that it fits fairly snugly into the tube. The corona in *H. triebneri* is almost exactly as in *H. ruschii*, both in size and in structure.

This species is very closely related to *H. ruschii* and the differences between them are discussed under *H. ruschii*.

History

Hoodia triebneri was discovered in 1933 by Wilhelm Triebner east of Swakopmund.

It has generally been accepted (White & Sloane 1937; Huber 1967; Plowes 1982) that *H. triebneri* Schuldt is a *nomen nudum* i.e. a name that was not validly published. If this were accepted, then there would be no need for *Trichocaulon triebneri* Nel to be given a new name on transfer to *Hoodia*, as Plowes (1992) did.

It may on the other hand be argued that Schuldt did validate his name since he gave a statement of how, in his opinion, it was distinguished from other species of *Hoodia*: 'The new *Hoodia triebneri* generally departs from the other Hoodias by its dwarfish habit, as the plants reach only 10-20 cm in height.' This is sufficient to constitute valid publication. However, he published two photographs of his species, of which the upper one is *H. juttae* and the lower is *H. gordonii*. His concepts of the species were therefore extremely confused and his possibly diagnostic statement is in fact quite useless for distinguishing his 'species' from any other. Thus I am inclined to the traditional view that *H. triebneri* Schuldt is a *nomen nudum*. This obviates the need for a new name and also preserves the epithet 'triebneri' for these plants, which is the name by which they are mostly known.



Fig. 449. *H. triebneri*, PVB 3632, Otjimbingwe, Namibia.



Fig. 450. *H. triebneri*, PVB 3632, Otjimbingwe, Namibia

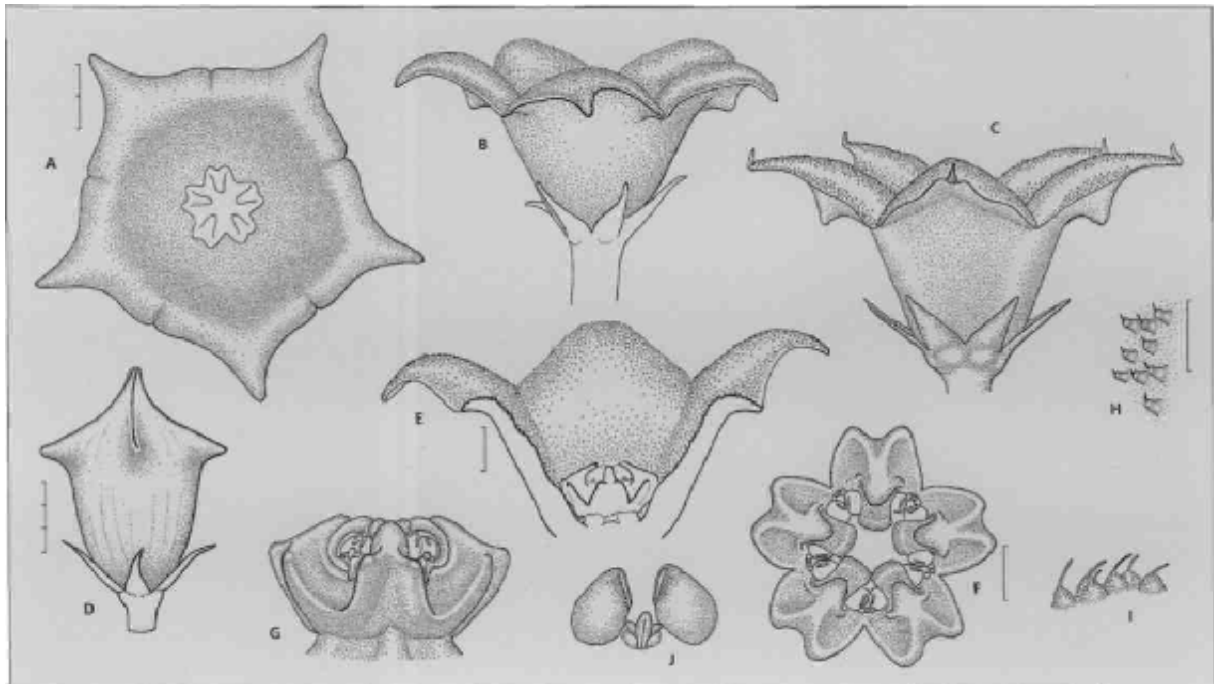


Fig. 451. *Hoodia triebneri*. A, face view of flower. B, C, side view of flower. D, bud. E, side view of dissected flower. F, face view of gynostegium. G, side view of gynostegium. H, I, papillae inside corolla with apical hairs directed towards tips of lobes: H, in tube; I, on lobe. J, pollinarium. Scale bars: A-C, 2 mm (at A); D, 3 mm; E, 1 mm; F, G, 0.5 mm (at F); H, I, 0.5 mm (at H); J, 0.25 mm (at H). Drawn from: C, D, H, I, PVB 3632, Otjimbingwe, Namibia; rest, *M. Visagie sub Giess 15303*, Gross Barmen, Namibia.

9. *Hoodia gordonii*

Hoodia gordonii (Masson) Sweet ex Decne, in DC, Prodr. 8: 665 (1844).

Stapelia gordonii Masson, Stap. Nov.: 24, t. 40 (1797).

Gonostemon gordonii (Masson) Sweet, Hort. Brit., ed. 1: 278 (1826).

Scytanthus gordonii (Masson) Hook., Hooker's Icon. Pl. 7: t. 625 (1844).

Type: South Africa, Namaqualand, near Orange River, R.J. Gordon (missing).

Lectotype: Masson, Stap. Nov.: t. 40.

Hoodia barklyi Thistleton-Dyer, J. Linn. Soc. Bot. 15: 252 (1876).

Type: South Africa, Karoo, 1873, Lycett comm. McGibbon & Barkly (K).

Hoodia bainii Thistleton-Dyer, Bot. Mag. 104: t. 6348 (1878).

Type: South Africa, Uityk on road to Beaufort West, autumn 1876, Bain I (K).

Hoodia albisipina N.E.Br., Fl. Cap. 4 (1): 900 (1909).

Type: South Africa, Carnarvon Div., Vanwyksvlei, Alston sub N.S. Pillans 18 (K, holo., BOL, iso.).

Hoodia burkei N.E.Br., Fl. Cap. 4 (1): 899 (1909).

Type: South Africa, Beaufort West district, near Gamka River, Burke 464 (K).

Hoodia pillansii N.E.Br., Fl. Cap. 4 (1): 898 (1909).

Type: South Africa, Prince Albert district, Grootfontein, Jan. 1904, N.S. Pillans 164 (K, holo.; BOL, iso.).

Hoodia rosea Obermeyer & Letty, Fl. Pl. South Africa 16: t. 615 (1936).

Type: South Africa, Cape, Rietvlei (Gordonia), Lang & E. Schweickerdt in Tvl Mus. 34896 (PRE).

Hoodia husabensis Nel in A.C. White & B. Sloane, Stap. 3: 1069 (1937).

Type: Namibia, Husab gorge, June 1935, Boss sub SUG 6920 (missing).

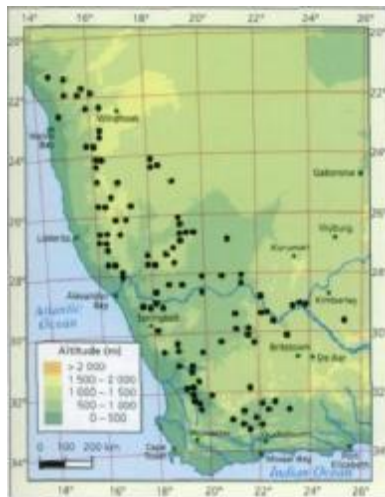


Fig. 453. Distribution of *Hoodia gordonii*.



Fig. 452. *H. gordonii*, south of Warmbad, Namibia, plants common in flat areas among scattered grass-clumps and bushes of *Rhigozum trichotomum*.

Lectotype: White & Sloane, Stap., ed. 2, 3: fig. 1145.

Hoodia langii Obermeyer & Letty in A.C. White & B.

Sloane, Stap., ed. 2, 3: 1067 (1937).

Type: South Africa, about 90 miles west of Upington, April 1933, Lang & E. Schweickerdt sub Tvl Mus. 32843 (PRE).

Hoodia longispina Plowes, Brit. Cact. Succ. J. 11: 57 (1993).

Type: Namibia, 4-5 km south of Witputz, Plowes 5321 (SRGH).

Many-stemmed shrub to 1 m tall and 0.6 m broad. Stems 0.1-1.0 m long, 25-50 mm thick, erect, grey-green to grey-brown; tubercles prominent, fused in lower half into 11-17 obtuse angles along stem, each tipped with a sharp spine 6-12 mm long. Inflorescences each with 1-4 flowers, opening successively; pedicel 8-30 mm long, 2-3 mm thick, oval in cross-section; sepals 5-6 mm long, 2-4 mm broad at base, ovate-lanceolate and overlapping at bases, acuminate, adpressed to corolla. Corolla (40-) 50-100 mm diam., ± rotate, ± circular to quite clearly 5-lobed; outside pale flesh-coloured with darker veins; inside flesh-coloured to deep purple-red usually with darker veins, smooth to covered with small conical papillae (sometimes red around mouth of tube) each tipped with a bristle up to 2.0 (-2.5) mm long; tube 1.0-1.5 mm long, 4.5-6.0 mm broad at mouth, containing most of gynoecium, formed entirely by annular thickening near base in otherwise ± flat corolla; lobes up to 15 mm long (excluding narrow tip), 50 mm broad at base, spreading, broadly ovate, abruptly narrowing to subulate point 3-6 mm long. Corona 1.5-2.0 mm tall, 4-6 mm broad, purple-black, glabrous, usually just touching side of tube at mouth, raised on very short stipe; outer lobes erect, entire and truncate or emarginate to bifid up to halfway down into ascending obtuse lobules < 1 mm long, laterally fused for most of length to bases of inner lobes; inner lobes ± 1 mm long, adpressed to backs of anthers and usually slightly exceeding them, linear to ± square, obtuse to truncate, with broad dorsal ridge near base connecting them to outer lobes.

Distribution and habitat

Hoodia gordonii is extremely widely distributed. It is found from the Brandberg in Namibia (about 21°S) southwards into the Northern and Western Cape, where it is of scattered occurrence over much of the Great Karoo to the Ceres Karoo in the south-west and the Prince Albert district (33°S) in the extreme south. It is found as far east as near Kimberley in the Northern Cape and near Fauresmith in the Free State as well as in south-western Namibia. Generally *H. gordonii* avoids the winter-rainfall areas, only occurring towards their drier margins where some summer rainfall is received - for example it is hardly recorded at all from Namaqualand. Exceptions to this are found along the Doom River from north of Tulpfontein to Doringbos, on the Ceres Karoo and along the northern margins of the Cedarberg. This is also the only area where it will be found occasionally growing on soils derived from sandstones. Apart from winter-rainfall, another limiting factor appears to be frost, to which *H. gordonii* is very susceptible. As a consequence, it is absent from many of the higher areas of the Roggeveld Plateau, for example.

With such an enormous range the species grows in a wide variety of habitats from very dry, rocky places to sandy spots in riverbeds. Plants often form quite extensive colonies of robust shrubs and larger specimens grow in the open, having long outgrown the protecting shrub in which they generally start off as a seedling.

Hoodia gordonii is usually a common plant where it occurs and there are many vast, barren areas (such as parts of Bushmanland, the central Ceres Karoo and places in south-eastern Namibia) where it is almost the only plant to be seen.

HOODIA GORDONII

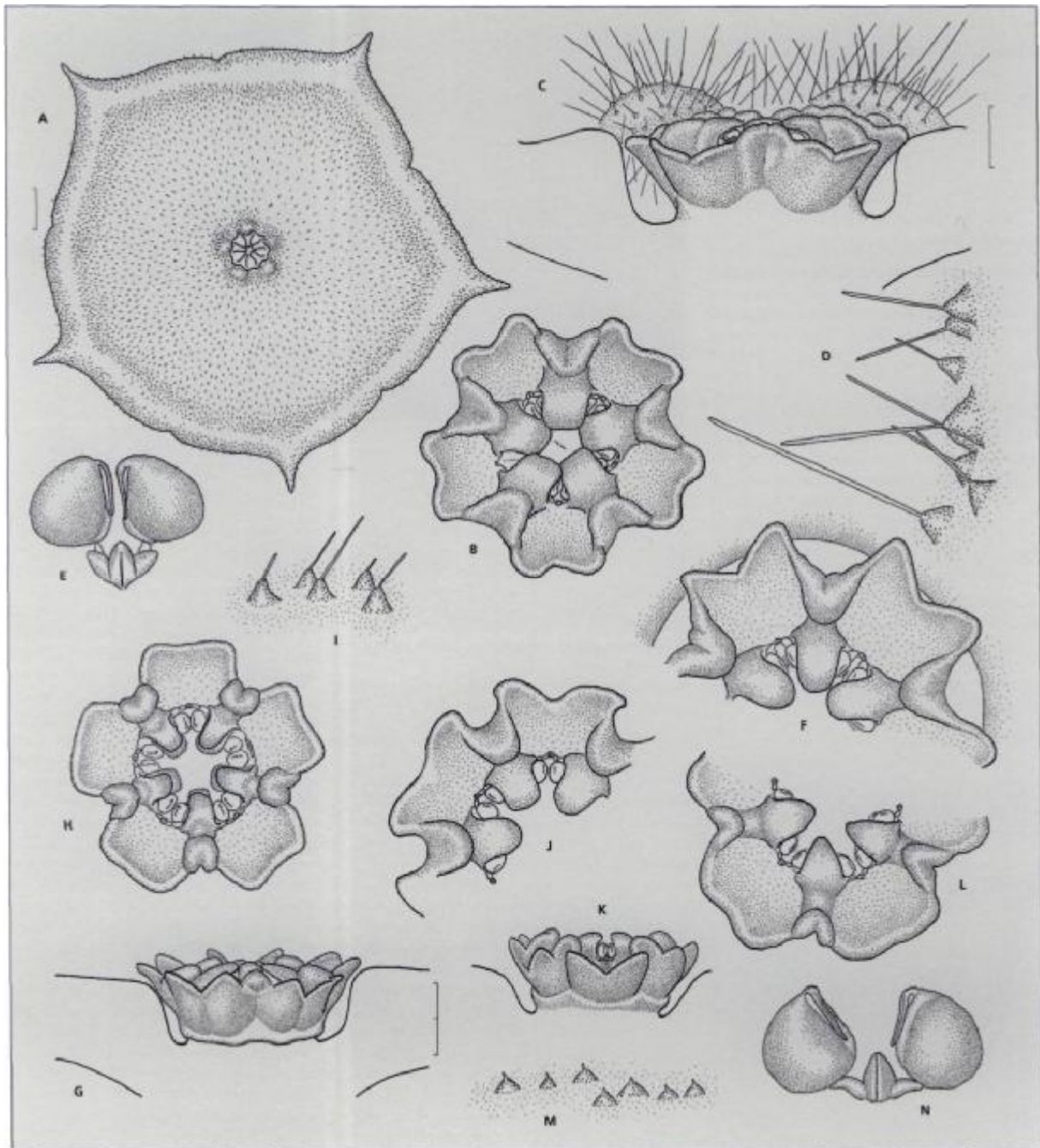


Fig. 454. *Hoodia gordonii*. A, face view of flower. B, F, H, J, L, face view of gynostegium (or part of it). C, G, K, side view of gynostegium. D, I, M, papillae inside corolla beyond mouth of tube. E, N, pollinarium. Scale bars: A, 5 mm; B, C, F, H, J, L, 1 mm (at C); G, K, 2 mm (at G); D, I, M, 0.5 mm (at C); E, N, 0.25 mm (at C). Drawn from: A-E, *Cole 101*, east of Aroab, Namibia; F, G, *PVB 2620*, 67 km north of Karooport; H, I, *PVB 3575*, Springboktrek Suid, near Koes, Namibia; J, K, *PVB 2720*, near Umduus; L-N, *PVB 2621*, Elandslei, Ceres Karoo.



Fig. 4.55. *H. gordonii*, PVB 3507, south-eastern flank of the Great Karas Mountains, Namibia, with small, white spider waiting for visitors (cf. fig. 13.79), in habitat, January 1989.



Fig. 4.56. *H. gordonii*, PVB 5694, (Dis nou) Vergenoeg, western side of the Tiras Mountains, Namibia, in habitat, March 1993.



Fig. 4.57. *H. gordonii*, PVB 5694, (Dis nou) Vergenoeg, western side of the Tiras Mountains, Namibia, March 1993. This and the previous picture give some idea of the variability of this species in one locality.

Diagnostic features and relationships

Plants of *H. gordonii* form robust shrubs, usually about as broad as tall, with many erect, densely clustered stems which mainly branch from the base. Though the bases of the stems are all very close to, if not in contact with the soil, no rooting takes place on the side-branches. The stems are sharply spiny and difficult to handle.

When enough rain is received, these otherwise dull grey, spiny shrubs become transformed. Flowering may be then so profuse that the stems are completely hidden by the flowers.

In most areas flowers of *H. gordonii* vary from pale flesh-pink to somewhat yellowish, with the colour fading to pinkish as the flower ages. Much greater variation, from intense purple-red to the usual flesh-pink colour is found in populations between the Naukluft and the Tiras Mountains in western Namibia. The same deep purple-red colour has also been observed near Gochas in the Auob River valley, which lies on the eastern side of Namibia and along the edge of the Kalahari. These deeper colours also tend to fade as the flowers age.

Flowers of this species are very variable in size. In cultivation such variation has a lot to do with the state of health of the plant, as a specimen which has not rooted properly will often produce abnormally small flowers. Flowers also decrease in size as the flowering period advances, with the largest often appearing first. There is also much variation from plant to plant and, in any population of reasonable size, flowers between 50 and 100 mm in diameter can usually be found.

There is also much variation in the shape of the flowers: in some the united portion beyond the annulus may be deeply cup-shaped while in others it is only shallow or nearly flat to even slightly convex. The lobes vary from very indistinct (so that the flower is almost circular in outline) to clearly defined, which lends the flower a definite five-lobed shape, although this is not usually as clear as in some forms of *H. currorii*.

In *H. gordonii* the corolla tube is usually somewhat pentagonal in outline. The tissue around its mouth is thickened and raised into five slight mounds opposite the anthers. Towards the centre the flower often becomes paler, though sometimes it is darker if covered with reddish papillae, with the raised area at the mouth of the tube always significantly paler than beyond and so highlighting the purple-black corona. This is different from *H. currorii* where the mouth of the tube is darker than the surrounding tissue and is noticeably shiny.

In many plants of *H. gordonii* the interior of the corolla is somewhat papillate. These papillae usually have an apical bristle which varies from extremely short to 2 mm long or even longer on rare occasions. In the southern part of the distribution such papillae are rarely found and, for example, in one large colony on the Ceres Karoo, only one plant was seen with them. Here the papillae were bright red and so they were clearly visible against the flesh-coloured background of the corolla. Further northwards

the flowers become steadily more frequently papillate and over most of Namibia papillate flowers predominate. However, even here there is a tendency for flowers to vary greatly from smooth to papillate without bristles or to papillate with quite long bristles, in which case the flower has an almost hairy appearance. In the winter-rainfall part of Namibia (the extreme south-west) smooth-flowered plants are again common but occasionally papillate ones occur and at several spots east and south of Witpütz quite conspicuously 'hairy-flowered' plants have been reported several times and these were even recently described as a new species, *Hoodia longispina*.

From the various forms of *H. currorii* in central western Namibia (Swakopmund northwards to Khorixas and eastwards to the Erongo Mountains) and Botswana, *H. gordonii* is usually easily separated when sterile by its erect, parallel stems that form a neat shrub. In *H. currorii* in these areas the stems have an untidy, spreading habit. Florally the two dif-



Fig. 4.58. *H. gordonii*, south of Warmbad, Namibia, in some flowering specimens such as this one the stems are completely hidden by the flowers, in habitat, January 2000.

HOODIA JUTTAE

fer significantly: *H. currorii* has much longer bristles on the corolla, a conspicuous shiny, livid mouth to the corolla tube and the gynostegium is completely contained within the tube, whereas in *H. gordonii* at least the top of the gynostegium protrudes from the tube and sometimes most of it is exerted. Also the respective coronas look rather different: in *H. currorii* the outer lobes are erect with incurved margins and they considerably exceed the height of the inner lobes, whereas in *H. gordonii* the outer lobes are spreading-erect without incurved margins and they do not exceed the height of the anthers.

One of the characters that appears to have given rise to an especially large amount of confusion is the presence or absence of papillae on the inside of the corolla. A good illustration of this problem is provided by comparing the accounts in Plowes (1982) and that in Plowes (1993), where the existence of such variation is at last acknowledged. Many of the names listed above as synonyms have been separated at one time or another on differences in the surface of the corolla and the latest example of this is the case of *H. longispina*. Plowes related this new species to *H. currorii*, largely because of the longer bristles on the corolla. As is pointed out above, this is not the main character separating the two and all other characters of his new species point to *H. gordonii*. In addition, such a relationship would make no biogeographical sense, in view of the well-documented distribution of the two species involved. In view of the wide variability of this and other characters in *H. gordonii*, this is regarded as an extreme example of this variation and reduced to synonymy.

History

Hoodia gordonii was discovered by Robert Gordon in 1779 somewhere near the Orange River and was named in his honour by Francis Masson. It is believed that the figure of *Stapelia gordonii* which appeared in Masson's *Stapeliae Novae* was by Gordon rather than Masson. As is the case with many of the easily collected species of stapeliad (such as *Stapelia grandiflora*, *S. hirsuta* and *Orbea lutea*), *H. gordonii* has a very extensive synonymy.

In fact *H. gordonii* has been subjected to more unjustified splitting than any other species in this genus and a great deal of nonsense has been written on how to separate all the various names sunk above. The reason for this chaotic state of affairs seems to lie mainly in collectors gathering single plants from populations which are then grown and, on flowering, found to differ in all manner of details. No attempt ever appears to have been made to observe whole populations in flower. Such observations would clarify how these details fit into general patterns of variation in this and other related species and thus how much relevance they ought to be accorded.



Fig. 4.59. *H. gordonii*, south of Merweville. Specimen with small, almost circular flowers.



Fig. 4.60. *H. gordonii*. PVB 5655, southern side of the Naukluft, Namibia. Plants with dark flowers like these are found in many parts of southern Namibia, in habitat, March 1993.

10. Hoodia juttae

Hoodia juttae Dinter, *Neue Pflanzen Deutsch-SWA's* 34, fig. 25 (1914).

Hoodia bainii var. *juttae* (Dinter) H. Huber, *Mitteil. Bot. Staatssamml. München* 4: 33 (1961).

Type: Namibia, Klein Karas, J. Dinter 3203 (SAM, holo.; S, iso.).

Many-stemmed shrublet to 0.3 m tall, 0.5 m broad. Stems 60-300 mm long, 30-50 mm thick, erect, pale grey-green; tubercles prominent, fused in lower half into 15-17 obtuse angles along stem, each tipped with a stiff spine 8-11 mm long. Inflorescences each with 1-4 flowers opening successively, pedicel 10-30 mm long, 2.5-4.0 mm thick, slightly oval in cross-section; sepals 3-5 mm long, $\pm$ 2 mm broad at base, acuminate. Corolla 20-55 mm diam., $\pm$ rotate, flat to very shallowly saucer-shaped, slightly and broadly 5-lobed; outside pale yellow-brown; inside pale yellow-brown to dark flesh-pink with darker veins, slightly depressed around corona lobes outside tube, without papillae; tube 1 mm long, 2.5-3.5 mm broad at mouth, cupular, formed entirely by annular thickening near base in otherwise $\pm$ flat corolla; lobes 4-8 mm long (excluding narrow tip), 15-25 mm broad at base, spreading, broadly ovate obtuse, abruptly narrowing to subulate point 2-5 mm long. Corona $\pm$ 2 mm tall, 3.0-4.5 mm broad, dark purple-black, glabrous, raised on short stipe; outer lobes $\pm$ 1.0 mm long, 1.5 mm broad, erect then spreading so that tips touch corolla, transversely oblong to shortly bifid, truncate-emarginate to obtuse, laterally fused near base to bases of inner lobes; inner lobes $\pm$ 0.5 mm long, linear to $\pm$ square, obtuse to truncate, usually slightly overlapping laterally near tips, with obtuse dorsal projection fused to outer lobes.

Distribution and habitat

Hoodia juttae is known only from around the base of and within the Little and Great Karas Mountains of southern Namibia. In the Great Karas Mountains it occurs both around the foot of the mountains and also on many of the high, flat-topped summits that make up this range. After the excellent rains which fell

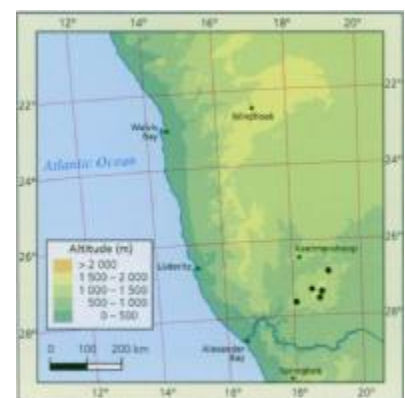


Fig. 4.61. Distribution of *Hoodia juttae*.

in December 1988 in this region, many plants were seen in flower and it was found to be not particularly rare.

Specimens grow among rocks and short bushes, often in the open.

Diagnostic features and relationships

Hoodia juttae is interesting from a taxonomic point of view. While flowering specimens look remarkably distinctive, actually the differences between them and the ubiquitous *H. gordonii* are subtle and small. In addition it occurs together with *H. gordonii* in many places in the Great Karas Mountains. Both species were seen flowering profusely with no trace of intermediates or hybrids. Vegetatively there is not much difference between them. In *H. juttae* the stems are often a bit stouter, they never attain the height of those in *H. gordonii* and the plant has a slightly more compact habit, often broader than tall.



Fig. 4.62. *H. juttae*, PVB 3508, Great Karas Mountains, Namibia. A large specimen which shows some variation in flower-colour as the flowers age, in habitat, January 1989.

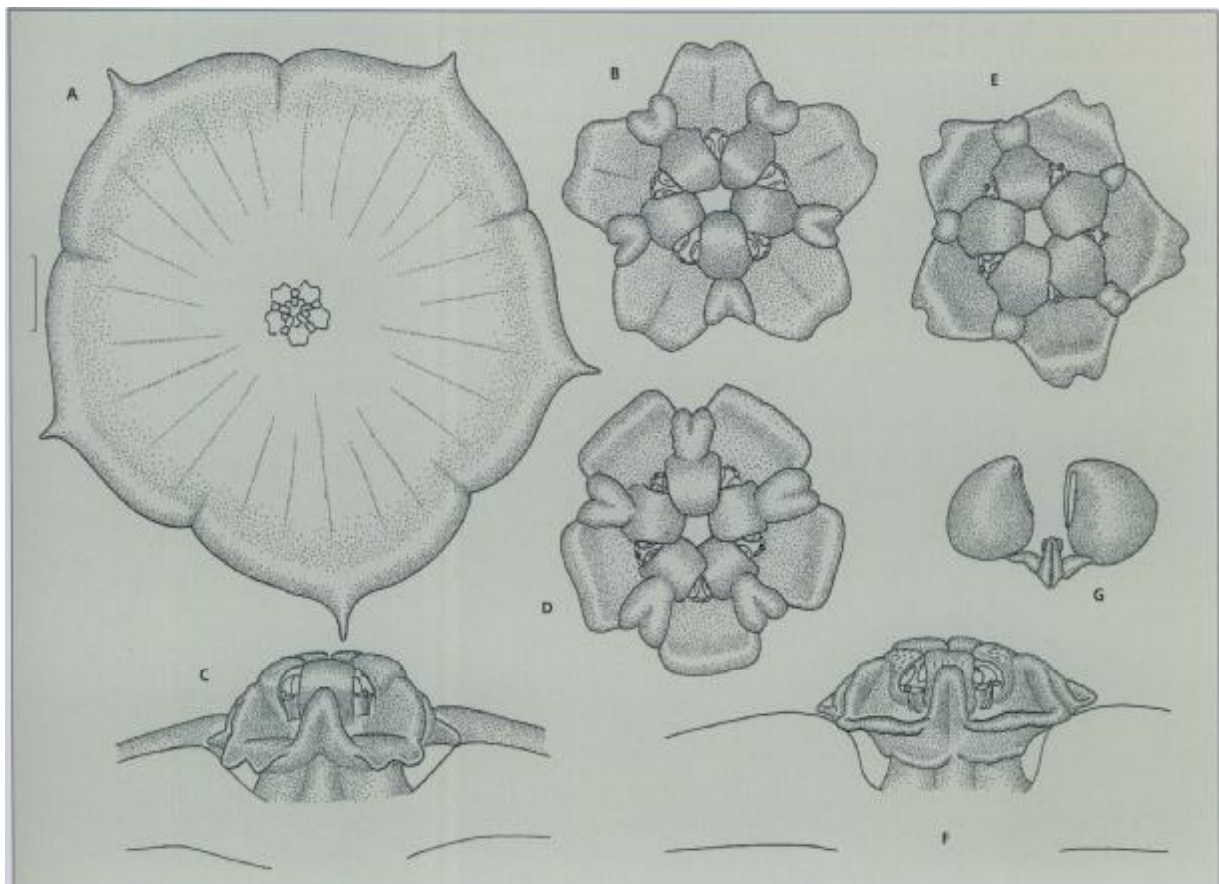


Fig. 4.63. *Hoodia juttae*. A, face view of flower. B, D, E, face view of gynostegium. C, F, side view of gynostegium. G, pollinarium. Scale bars: A, 5 mm; B-F, 1 mm (at A); G, 0.25 mm (at A). Drawn from: A-C, PVB 3508, Great Karas Mountains, Namibia; D-G, PVB 3526, central Great Karas Mountains, Namibia.



Fig. 4.64. *H. juttae*, PVB 3508, Great Karas Mountains, Namibia.



Fig. 4.65. *H. juttae*, PVB 3508, Great Karas Mountains, Namibia, specimen with almost circular flowers and very short outer corona lobes.

Florally there are various arcane differences. The flowers of *H. juttae* are always much smaller than those of *H. gordonii*. Those of *H. gordonii* may also be small but this is usually due to lack of water or ill health and under these conditions *H. juttae* produces flowers as small as 20 mm across, which is far smaller than any seen as yet in *H. gordonii*. In *H. juttae* the flowers are held roughly erect and well away from the stem on a relatively long, thick pedicel while in *H. gordonii* they are held closer to the stem with a tendency to wrap around it and cover it up when produced in numbers. In *H. juttae* the inside of the flowers is variable in colour from yellow-brown to a deep flesh-pink and the veins are always clearly visible (in *H. gordonii* in this area they are a much paler flesh-pink). The flowers show the usual variation for the large-flowered species, from circular to quite deeply five-lobed (cf. figs. 4.65 and 4.64).

The main difference between the two lies in the corona. In *H. juttae* the outer lobes form only a shallow cup with the lobes spreading and actually adpressed to the surface of the corolla

just outside the tube. They spread away from the gynostegium more or less horizontally at the same level as the surface of the corolla. On the other hand, in *H. gordonii* they form a pouch much lower on the gynostegium and rise up from this level to touch the side of the corolla tube obliquely and they do not lie on the surface at its mouth. This relatively inconspicuous difference leads one to suspect that Huber's treatment of *H. juttae* as a variety of *H. bainii* (= *H. gordonii*) is eminently sensible. Nevertheless I prefer to maintain this taxon as a separate and distinct species, especially in view of its intimately interlinked distribution with *H. gordonii* and the fact that no intermediates at all were found between them.

History

Hoodia juttae was discovered at Klein Karas by Jutta Dinter in October 1913 and named by her husband for her. It has been collected relatively rarely and consequently there are few records of it.



Fig. 4.66. *H. juttae*, PVB 3526, central Great Karas Mountains, Namibia, a dark-flowered specimen, in habitat, January 1989.

11. Hoodia dregei

Hoodia dregei N.E.Br., Fl. Cap. 4 (1): 897 (1909).

Type: South Africa, Cape, between Dweka and Swartbulletjie, Drege 5616 (K).

Shrublet with 3-8 or more stems. Stems 60-200 (-500) mm long, 25-60 mm thick, erect, brownish green; tubercles prominent, fused in lower half into 16-24 acute angles along stems, each tipped with a weak spine 5-7 mm long (dark purple-brown when young). Inflorescences each with 1-5 flowers opening successively, pedicel 7-12 mm long, 2-3 mm thick; sepals 3-4 mm long, 1.5 mm broad at base, lanceolate-subulate. Corolla 28-48 mm diam., ± rotate, flat to saucer-shaped, slightly and broadly 5-lobed; inside dark flesh-coloured to greenish yellow becoming pinkish red near centre, densely covered with soft white hair-like bristles 1-3 mm long each arising from a small maroon-tipped cylindrical obtuse papilla; tube 1 mm long, 3.5-4.0 mm broad at mouth, cupular, pentagonal, formed by annular thickening near base in otherwise ± flat corolla, this thickening raised into 5 pinkish slightly shiny bulges around its mouth; lobes 4-7 mm long (excluding narrow tip), 12-18 mm broad at base, spreading, broadly ovate, obtuse, abruptly narrowing to attenuate subulate point 3-6 mm long. Corona ± 2.5 mm tall, 3-4 mm broad, dark purple-black, glabrous, raised on short stipe; outer lobes 0.5-1.0 mm long, 10-17 mm broad, spreading, transversely oblong, truncate-emarginate to shortly and obtusely bifid, laterally fused near base to bases of inner lobes; inner lobes ± 0.5 mm long, ± square to deltoid, obtuse to truncate, not exceeding anthers, with obtuse dorsal projection fused to outer lobes.

Distribution and habitat

Hoodia dregei is a rare species which is found only in the south-western portion of the Great Karoo between Merweville, Beaufort West and Prince Albert.

Plants grow on stony slopes of hills or on stony flat areas, where they may be partly hidden inside a bush or may grow in the open among stones.

Diagnostic features and relationships

In the field, plants of this species are usually small, rarely exceeding 200 mm tall and consisting of only a few stems. The stems sometimes have a spreading habit but they

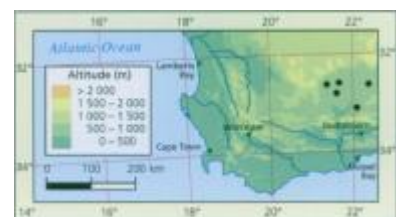


Fig. 4.67. Distribution of *Hoodia dregei*.



Fig. 4.68. *H. dregei*, PVB 4817, south-west of Merweville, plant in habitat in a season of good rains. The slender tips of the corolla lobes are clearly visible here.



Fig. 4.69. *H. dregei*, PVB 4817, south-west of Merweville.

are markedly thicker (for their length) than in the other species with large flowers to which it is related. With 16-24 rows of tubercles, the stems have many more angles than in any of its closest relatives, where the stems are normally 11-17-angled. They generally also have noticeably weaker spines on the tubercles than the other species and these spines tend to wear off with age.

In outline the flowers of *H. dregei* are circular to very slightly five-lobed. Each corolla lobe is quite a bit broader than long and suddenly narrows into a slender, attenuated point. The inside of the flower is covered densely with fine, white, usually somewhat crinkled hairs up to 3 mm long, which lends it a distinctly woolly appearance. Each of these hairs arises at the apex of a small, cylindrical papilla and represents a much modified apical cell exactly as do the much shorter versions in species like *H. gordonii* or *H. pilifera*. The corolla itself is

flesh coloured but this is somewhat modified by the colour of these hairs and also by the fact that the apex of each papilla is maroon. Towards the centre the colour of the corolla changes to pinkish red. Here there is a short tube which is free of papillae and hairs and this tube is formed by a thickening in the otherwise flat centre of the corolla. The mouth of the tube is often emphasised by five bulges which lie below the sinuses of the lobes and it is generally somewhat shiny.

The slightly shiny, blackish corona stands in the centre, well separated from the sides of the tube since it is somewhat smaller in diameter than the tube. It consists of a shallowly cup-shaped outer corona with broad, truncate lobes and broad inner lobes incumbent on but not exceeding the anthers. The outer lobes spread perpendicular to the axis of the flower, usually somewhat above the annulus at the mouth of the corolla tube.

Vegetatively, on account of the thicker, many-angled stems and weaker spines, *H. dregei* is rather more similar to species of the former sect. *Trichocaulon* than to the other large-flowered species. However, the shapes of the buds, the flowers and the corona clearly indicate that it belongs among these species. The hairiness of the flower suggests a close affinity to *H. currorii*, though other features of the flower and their respective distributions seem to suggest an affinity with *H. gordonii*.

History

Hoodia dregei was discovered by J.F. Drège in March 1827 north of Prince Albert. After that there were no more records until it was rediscovered nearly 100 years later in 1924 near Merweville by the palaeontologist Robert Broom. Even today, it remains known from very few collections.



Fig. 4.70. *H. dregei*, PVB 4817, south-west of Merweville, specimen with somewhat yellowish corolla.

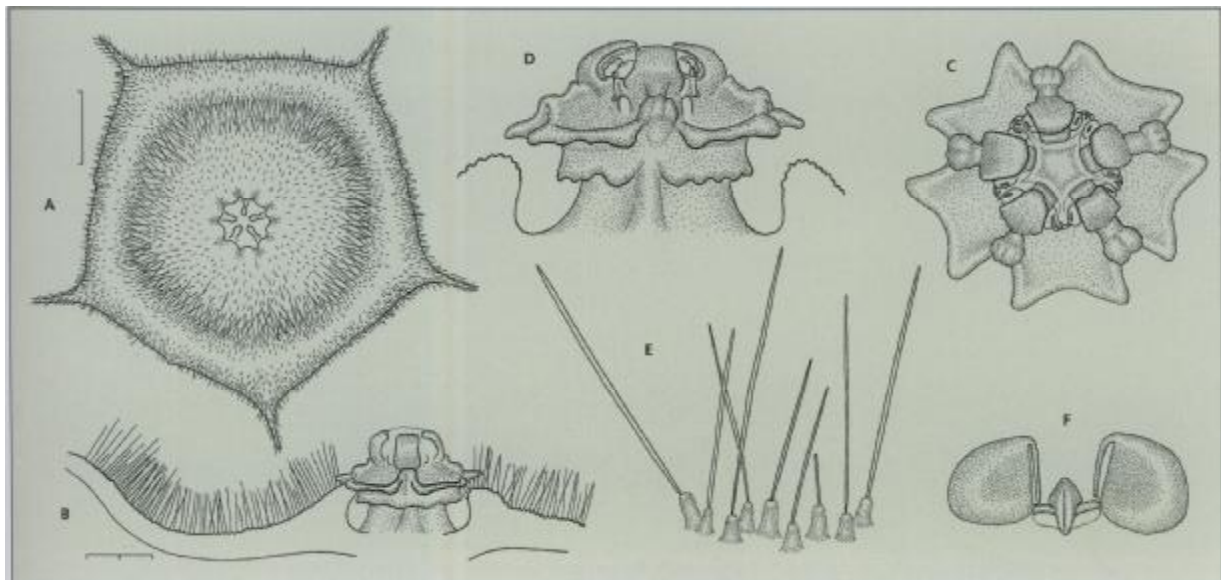


Fig. 4.71. *Hoodia dregei*. A, face view of flower. B, side view of centre of dissected flower. C, face view of gynostegium. D, side view of gynostegium. E, papillae inside corolla. F, pollinarium. Scale bars: A, 5 mm; B, 2 mm; C, D, 1 mm (at A); E, 0.5 mm (at A); F, 0.25 mm (at A). Drawn from: PVB 1258, south-east of Merweville.

12. Hoodia currorii

Hoodia currorii (Hook.) Decne, in DC, *Prodr.* 8: 665 (1844).

Scytanthus currorii Hook., *Hooker's Icon. Pl.* 7: t. 605-606 (1844).

Type: Angola, barren, sparingly sandy mountains at Elephant's Bay, A.B. *Curror* (K).

Many-stemmed shrub 0.15-1.00 m tall and 0.15-1.00 m or more broad. Stems 0.1-1.0 m long, 40-60 (-80) mm thick, erect to ascending, pale grey- to brown-green; *tubercles* prominent, fused in lower half into 11-16 (-24) obtuse angles along stem, each tipped with a sharp spine 6-10 mm long. *Inflorescences* each with 1-4 flowers opening successively; *pedicel* 3-50 (-60) mm long, 2-6 mm thick, oval in cross-section; *sepals* 4-8 mm long, 3 mm broad at base, ovate-lanceolate, acuminate, adpressed to corolla. *Corolla* 40-180 mm diam., $\pm$ rotate to concave-rotate, $\pm$ circular to broadly 5-lobed; outside pale flesh-coloured usually with narrow red-pink patch at base of tube among sepals; inside brick-red to flesh-pink or yellowish pink usually with darker veins, with bright livid orange-pink to red-pink shiny area around mouth and inside tube, with pink to purple hair-like bristles 0.5-3.5 mm long each arising from a dome-shaped papilla (papillae becoming larger towards lobes and vanishing towards centre, hairs longest towards centre); *tube* 2.8-6.0 mm long, 5-9 mm broad at mouth, pentagonal, with corolla thickened and raised into 5 mounds to form mouth, containing whole of gynostegium and much broader than

it; *lobes* 5-25 mm long (excluding narrow tip), 20-75 mm broad at base, spreading, broadly ovate to broadly deltate, abruptly narrowing into narrow subulate point 6-20 mm long. *Corona* 2-3 mm tall, 3.8-5.0 mm broad, deep red-purple or red-brown, shiny, glabrous to sparingly pilose outside, well separated from side of corolla tube, $\pm$ sessile; outer *lobes* erect, forming 5-lobed cup from slightly taller than style-head to nearly twice as tall as style-head, bifid for less than half of length into erect obtuse-truncate to deltoid teeth with outer margin folded inwards, fused laterally for most of length to bases of inner lobes; *inner lobes* $\pm$ 0.5 mm long, $\pm$ rectangular, obtuse, mostly exceeding anthers.

Two subspecies are recognised. One is distributed along the north-western flank of Namibia and southern Angola and the other is found in eastern Botswana, southern Zimbabwe and the northern part of South Africa. Such disjunctions are not unknown in other families of flowering plants and similar distributions exist in species of *Acacia* (*A. albida*, *A. kirkii*), *Androstachys johnsonii* and even in the widespread *Colophospermum mopane* (Coates Palgrave 1977).

12a. Hoodia currorii subsp. currorii

Hoodia macrantha Dinter, *Neue Pflanzen Deutsch-SWA's*: 35, fig. 52, 53 (1914).

Type: Namibia, Onguati am Fusse der Erongo-berge, Dinter 1648 (SAM).

Hoodia gibbosa Nel in A.C. White & B. Sloane, *Stap.*, ed. 2, 3:1061 (1937).

Type: Namibia, Sphinx, $\pm$ 70 miles east of Swakopmund, Boss sub SUG 6921 (NBG).

Hoodia montana Nel in A.C. White & B. Sloane, *Stap.*, ed. 2, 3:1063 (1937).

Type: Namibia, Brandberg, Nov. 1935, Nel sub SUG 6916 (missing).

Hoodia currorii var. *minor* R.A.Dyer, *Fl. PL Africa* 37: t.1474 (1966).

Type: Namibia, 26 miles north-east of Henties Bay, Hardy & De Winter 1508 (PRE).

Key to the subspecies of *H. currorii*

Corolla (50-160-170 (180) mm diam., pedicel at least 12 mm long, plants from

Namibia or Angola

12a. subsp. *currorii*

Corolla 40-75 mm diam., pedicel 3-7 mm long, plants from east of 24°E

12b. subsp. *lugardii*

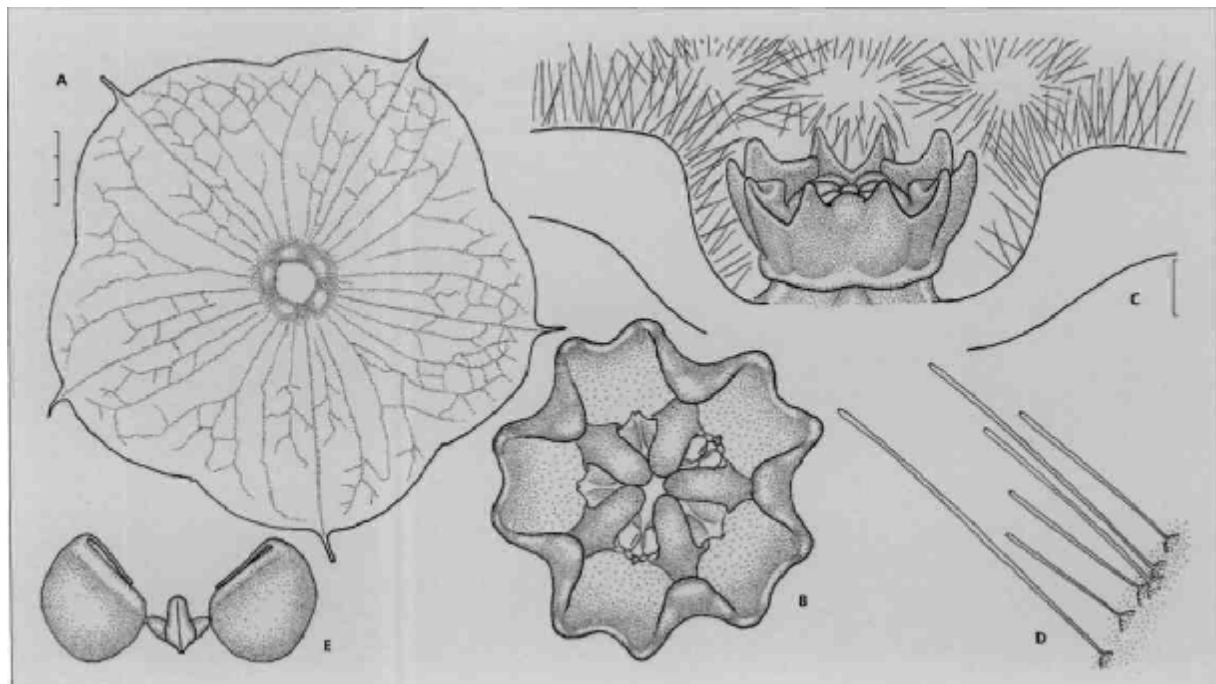


Fig. 4.72. Hoodia currorii subsp. currorii. Material from Damaraland with somewhat shallow corolla tube. **A**, face view of flower. **B**, face view of gynostegium. **C**, side view of centre of dissected flower. **D**, papillae inside corolla beyond mouth of tube. **E**, pollinarium. Scale bars: A, 15 mm; B, 1 mm (at A); C, 1 mm; D, 0.5 mm (at A); E, 0.25 mm (at A). Drawn from: PVB 4060, west of Kamanjab, Namibia.

Stems grey- to brown-green. Pedicel 12-50 (-60) mm long, 4-6 mm thick. Corolla (50-) 60-170 (-180) mm diam, rotate to concave-rotate; inside brick-red to flesh-pink or yellowish pink; tube (2.8-) 3.0-6.0 mm long, 6-9 mm broad at mouth; lobes $\pm$ 10-25 mm long (excluding narrow tip), 55-75 mm broad at base, with narrow subulate point 6-20 mm long. Corona 2-3 mm tall, 3.8-5.0 mm broad.

Distribution and habitat

Hoodia currorii subsp. *currorii* is found from 13°S in Angola to just below 23°S, which is a little south of Walvis Bay in Namibia. In Angola it appears to be restricted to the very arid parts

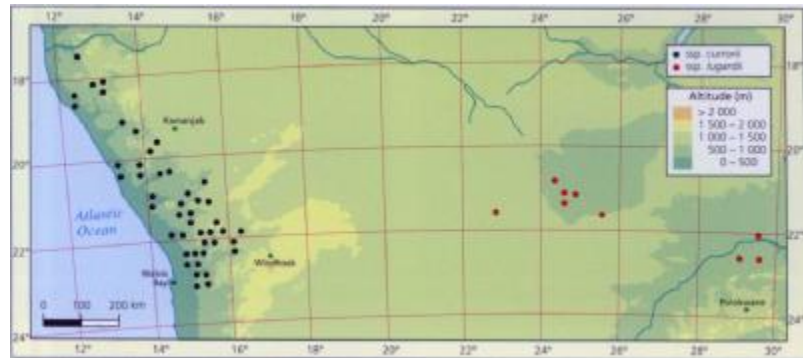


Fig. 4.73. Distribution of *Hoodia currorii* in southern Africa.

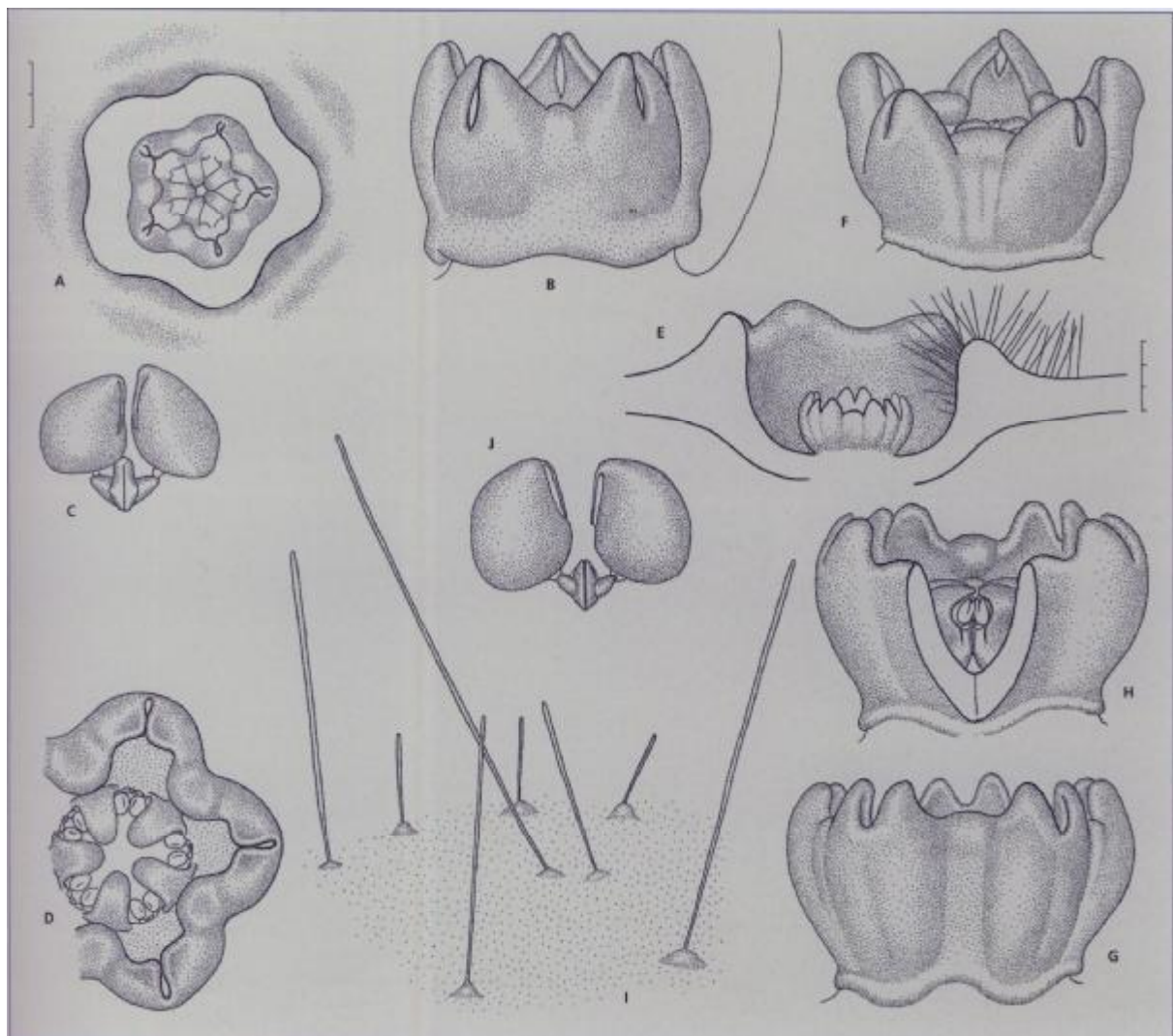


Fig. 4.74. *Hoodia currorii* subsp. *currorii*. Material from Namib Desert and Erongo Mountains with deeper corolla tube usually known as *Hoodia macrantha*. A, face view of centre of flower. B, F, G, side view of gynostegium. D, face view of gynostegium. E, side view of centre of dissected flower. H, gynostegium with one outer corona lobe cut away. I, papillae inside corolla beyond mouth of tube. C, J, pollinarium. Scale bars: A, 2 mm; B, D, F, G, H, 1 mm (at E); E, 3 mm; I, 0.5 mm (at E); C, J, 0.25 mm (at E). Drawn from: A-C, PVB 3624, Erongo Mountains, Namibia; D-J, PVB 3592, 33 km from Uis towards Usakos, Namibia.

HOODIA CURRORII



Fig. 4.75. *H. currorii* subsp. *currorii*, PVB 5621, west of Ozondati, Namibia.



Fig. 4.76. *H. currorii* subsp. *currorii*, Van Zanten 299, near Swakopmund, Namibia (photo: W. Bosma).



Fig. 4.77. *H. currorii* subsp. *currorii*, PVB 3595, Nainais, north of Usakos, Namibia, very large-flowered form from further inland than the next, in habitat, January 1989.



Fig. 4.78. *H. currorii* subsp. *currorii*, PVB 8063, south-west of Orupembe, Namibia, from near the coast in the Namib Desert, in habitat, December 1999.

of the coastal Namib Desert. In Namibia it also occurs in this arid zone but advances eastward as well. It occurs furthest east in dry *Colophospermum mopane* woodland of the Ugab River valley to the south-west of Outjo and more than 250 km from the coast. Records have also been made about 200 km from the coast in dry *Acacia* scrub in the Erongo Mountains and south-east of these beyond Karibib.

Plants are found mainly in fairly flat areas, growing in gravelly plains or among stones on low, rocky hills. They also occasionally grow in firm sand.

Diagnostic features and relationships

Many travelers in the Namib Desert north of Swakopmund in Namibia have encountered the large and spectacular forms of *H. currorii* that occur on the eastern edges of the desert and have been called traditionally *H. macrantha*. The plants form large shrubs up to 1 m in diameter and usually slightly less in height, with the stems spreading in a somewhat untidy manner. Despite their large size, they are surprisingly inconspicuous when not in flower.

After a good shower of rain the upper parts of the stems become covered with the intensely flesh-pink flowers. Flowering specimens are difficult not to see and are some of the most photogenic stapeliads that exist. The flowers may be enormous and have been recorded up to 180 mm across but are usually between 60 and 170 mm in diameter. In subsp. *currorii* the flower may be quite flat but it may also be shallowly bowl-shaped. Some are distinctly lobed and others have very obscure lobes. The inside of the corolla is covered with pink to purplish hairs up to 3.5 mm long which increase in length towards the centre of the flower. Outside, the flower is pale pinkish, usually with a ring of darker colour at the base among the sepals. On the inside it is red to flesh-pink which changes to a bright and shiny orangey pink just outside the mouth of the tube, where the surface is also much swollen, usually into five mounds. This tube is distinctly pentagonal around its mouth and is much taller than the gynostegium which sits in the base of it, quite isolated from its flanks.

Among the species of *Hoodia*, the gynostegium in subsp. *currorii* has comparatively tall outer corona lobes which are more or less erect and form a cup-like structure around the anthers. Their margins are incurved and they have a small notch in their apex. The inner lobes are small and not much longer than the anthers.

In northern Damaraland and on the western edges of the Kaokoveld plants of *H. currorii* have a rather different appearance. Here the stems are more neatly erect and packed into denser clumps so that the plants could easily



Fig. 4.79. *H. currorii* subsp. *currorii*, PVB 5543, near Sesfontein, Namibia.



Fig. 4.80. *H. currorii* subsp. *currorii*, PVB 5543, near Sesfontein, Namibia, with pale somewhat yellowish corolla.

be mistaken for *H. gordonii*. The colour of the flowers is usually also not so intense and, while they are usually also pink, somewhat yellowish ones have been seen in some spots around Sesfontein. In these plants (fig. 4.72) the corolla tube is generally shallower and the corona is also not as tall (this is true of material from Angola too). Nevertheless, the bright, shiny livid area around the mouth of the tube, the wide separation of the sides of the corolla tube from the gynostegium and the more cupular outer corona with incurved margins to the lobes all indicate that these plants belong to *H. currorii* rather than to *H. gordonii*.

History

Hoodia currorii was discovered by a naval doctor, A.B. Curror, when his ship, HMS *Water-Witch*, put in for water at Elephant's Bay in southern Angola in 1840. The plants

were described as *Scytanthus currorii* by W.J. Hooker in 1844 but in the same year were placed in *Hoodia* by J. Decaisne.

Several other names have been described (Plowes (1982) suggested that several more need to be described) and the most commonly used of these names is *H. macrantha* of Dinter. This name was given to large plants with particularly large flowers, which mainly occur around the foot of the Erongo Mountains. However, it was found (Bruyns 1993) that many of the dimensions (particularly the size of the plant and the size of the flowers) were closely matched by the type and other more recent collections from Angola. Photographs taken in Angola before the recent war broke out show that specimens growing in the area where the type was collected also have the somewhat spreading habit of *H. macrantha*. Therefore *H. macrantha* was made a synonym of subsp. *currorii*.



Fig. 4.81. *H. currorii* subsp. *currorii*, PVB 5543, near Sesfontein, Namibia. Plants in this area have more erect stems than those further south. The flowers are more variable in colour than in some other areas, as the previous two pictures show, in habitat, February 1993.

12b. Hoodia currorii subsp. lugardii

Hoodia currorii subsp. *lugardii* (N.E.Br.) Bruyns,
Bot. Jahrb. Syst. 115: 205 (1993).
Hoodia lugardii N.E.Br., *Fl. Trop. Afr.* 4 (1): 491 (1903).
Type: Botswana, Chukutsa Salt Pan, 2300', *Lugard* 303 (K).

Stems pale grey-green. *Pedice* 3-7 mm long, 2-6 mm thick. *Corolla* 40-75 mm diam., concave-rotate; inside brick-red to pale flesh-pink; *tube* $\pm$ 4 mm long, 5-6 mm broad at mouth; *lobes* $\pm$ 5-11 mm long (excluding narrow tip), 20 mm broad at base, with subulate point 5-7 mm long. *Corona* $\pm$ 2.5 mm tall, 4.0 mm broad.

Distribution and habitat

Hoodia currorii subsp. *lugardii* is found further east than any other *Hoodia* and grows in Botswana, Zimbabwe and in South Africa in Limpopo Province, north of the Soutpansberg. In Botswana it is known mainly in the relatively low-lying, calcareous region of the Makgadikgadi Pans between the villages of Rakops, Lethlakane and Nata, and it also occurs in the eastern corner of the country near Pont Drift (Hargreaves 1995) along the Limpopo Valley. In both Zimbabwe and Limpopo Province it is found only in the Limpopo Valley, in Zimbabwe west of Beit Bridge and in South Africa in the calcareous country between All-days, Waterpoort and Tshipise. Throughout its range it has been rarely collected but it seems to be much more common than the herbarium records indicate.

Plants grow on calcareous ground among grass tufts or small trees of *Acacia tortilis* and *Colophospermum mopane* in fairly open bushveld. They are often seen forming a shrub around the base of a tree.



Fig. 4.82. *H. currorii* subsp. *lugardii*, PVB 4471, near Alldays. The flowers usually have longer 'tails' on the corolla lobes than one finds in subsp. *currorii*.



Fig. 4.83. *H. currorii* subsp. *lugardii*, PVB 4471, near Alldays.

HOODIA CURRORII

Diagnostic features and relationships

Specimens of subsp. *lugardii* may cover an area as large as 1 sq m and the stems have a somewhat spreading habit similar to that in subsp. *currorii*. The plant usually has a rather paler grey colour than the Namibian subsp. *currorii*.

In subsp. *lugardii* the flowers are borne close to the stem on short, thick pedicels which do not exceed 7 mm in length. The flowers are 40-75 mm in diameter and are brick-red to pale pink inside.

Apart from the differing lengths of the pedicels, there is little on which to separate *H. lugardii* and *H. currorii*. Various minor distinctions can be found (Bruyns, 1993) but none of these is reliable. In view of the variation in *H. currorii* (especially in the size and shape of the flower but also in the height of the corona and the length of its lobes), the overall similarity between the plants, the similar corolla with the typically bright, livid area around the mouth of the tube and especially in the shape of the corona, *H. lugardii* was made a subspecies of *H. currorii*.

History

Subsp. *lugardii* was discovered by Major Edward Lugard in 1896 or 1897 in the low-lying calcareous region along the Botletle River, to the south of the Makgadikgadi Pans of central Botswana. In about 1943 it was collected for the first time in the valley of the Limpopo River in

South Africa north of the Soutpansberg. Plowes (1971) mentioned that it ought to occur in the rather similar country in southern Zimbabwe and this was confirmed in 1973 by a record made by L.C. Leach west of Beit Bridge. This remains the only collection known from Zimbabwe.



Fig. 4.84. *H. currorii* subsp. *lugardii*, PVB 4471, near Alldays. A large specimen about 1 m tall growing in the shade of a tree.

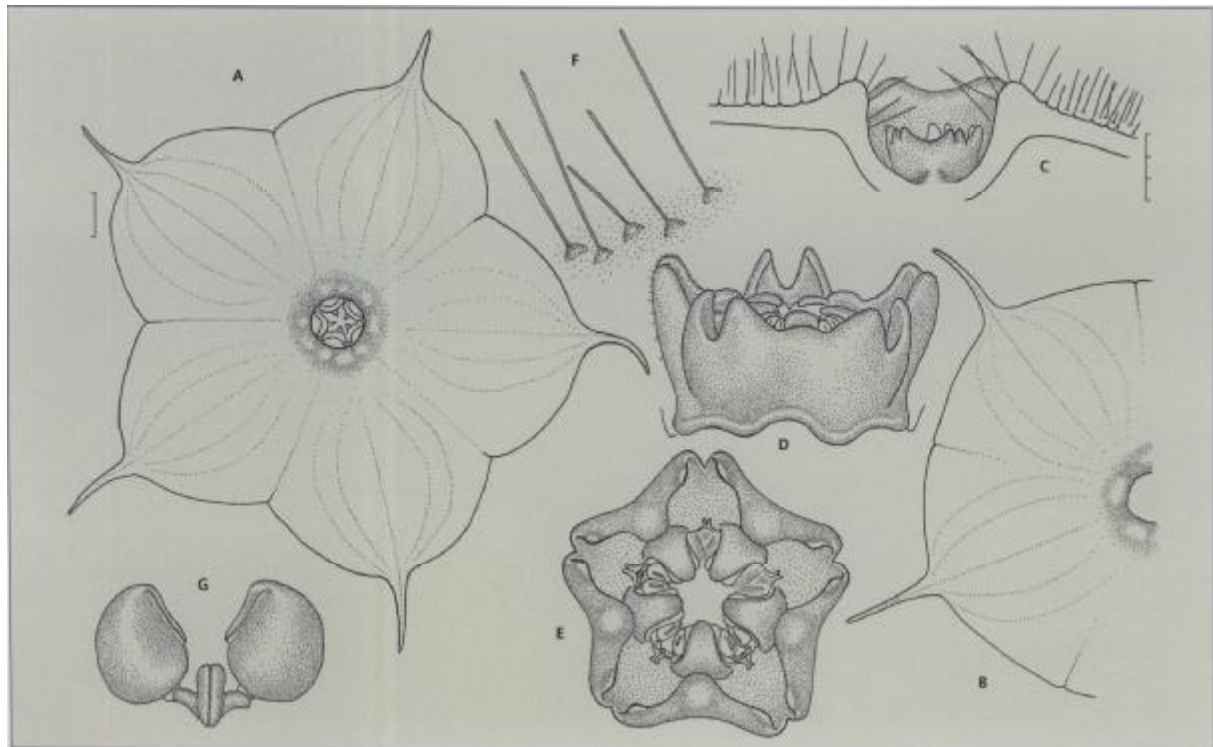


Fig. 4.85. *Hoodia currorii* subsp. *lugardii*. A, B, face view of flower. C, side view of centre of dissected flower. D, side view of gynostegium. E, face view of gynostegium. F, papillae inside corolla beyond mouth of tube. G, pollinarium. Scale bars: A, B, 5 mm (at A); C, 3 mm; D, E, 1 mm (at C); F, 0.5 mm (at C); G, 0.25 mm (at C). Drawn from: B, Leach 15085, north-west of Beit Bridge, Zimbabwe; rest Fourie 26446, near Messina.

13. *Hoodia parviflora*

Hoodia parviflora N.E.Br., Bull. Misc. Inform. 1895: 265 (1895).

Type: Angola, Mocamedes district, near Poman-gala, 1500', Welwitsch 4265 (K, holo.; G, iso.).

Few-to many-stemmed medium to large shrub, 0.3-2.2 m tall and 0.3-1.0 m broad. *Stems* 0.5-2.0 m tall, 35-110 mm thick, erect, usually strikingly matt bluish green (violet-green); *tubercles* prominent, fused in lower half into 14-18 obtuse angles along stem, each tipped with a stout spine 6-10 mm long. *Inflorescences* each with 1-4 flowers opening successively; *pedicel* 2-4 mm long, 3-4 mm thick, oval in cross-section; *sepals* 5-6 mm long, $\pm$ 3 mm broad at base, ovate-lanceolate, acuminate, adpressed to corolla in lower third only then spreading with reflexed tips. *Corolla* 30-55 mm diam., conical-campanulate, slightly 5-lobed; outside pale pink with darker veins; inside yellow to brownish orange (slightly darker in tube) with darker (usually reddish) veins, covered with low conical obtuse papillae each tipped with soft bristle up to 3.5 mm long; *tube* 3-4 mm long, $\pm$ 7 mm broad at mouth, broadly cupular, with mouth accentuated by thickening of corolla into 5 raised mounds, containing gynostegium; *lobes* $\pm$ 10 mm long (excluding narrow tip), 20-27 mm broad at base, spreading to recurved at tips, broadly ovate, abruptly narrowing into subulate point 5-7 mm long. *Corona* 2.0-2.5 mm tall,

4.0-4.5 mm broad, purple-black, glabrous, not touching sides of corolla-tube, raised on very short stipe; *outer lobes* erect, bifid to half-way down into erect deltoid to truncate obtuse lobules up to 1 mm long, laterally fused at least in lower half to bases of inner lobes; *inner lobes* $\pm$ 0.5 mm long, rectangular to deltoid, obtuse to truncate, shorter than anthers, with flattish dorsal projection near base connecting to outer lobes.

Distribution and habitat

Hoodia parviflora occurs in the south-western corner of Angola and in the adjacent north-western part of Namibia. In Angola it is known from the area west of the Chela Mountains and from the Iona Park. There are now quite a few collections from the Kaokoveld of Namibia and it is much more plentiful in Namibia than the records suggest. In fact it occurs more or less continuously from Ruacana Falls westwards down the valley of the Kunene river to Otjom-borombongo (west of the Baynes Mountains) and to Van Zyl's Pass and southwards to Okon-guati. It also occurs sporadically around Kaoko Otavi further south in the Kaokoveld.

Plants grow mostly in stony areas in river valleys but are also found widely scattered on steep slopes and mountain tops.

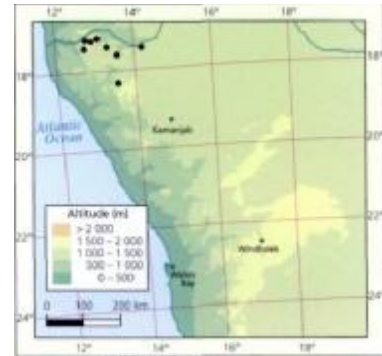


Fig. 4.86. Distribution of *Hoodia parviflora* in southern Africa.

In such steep spots (as in the valley around Otjomborombongo and in the Otjihipa), they grow among very scattered trees with *Euphorbia eduardoi* and clumps of the resurrection bush *Myrothamnus flabellifolius*. More usually they occur among the widely spaced trees of the arid *Colophospermum mopane* woodland that covers most of this area.

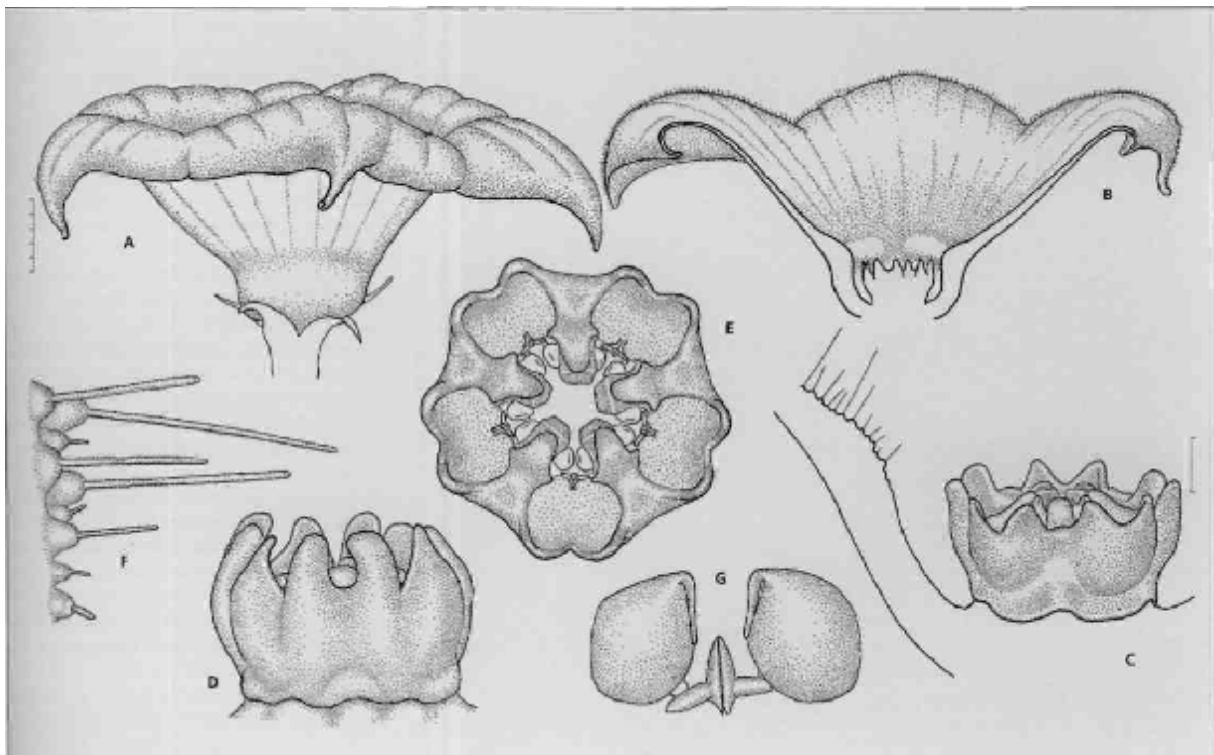


Fig. 4.87. *Hoodia parviflora*. A, side view of flower. B, side view of dissected flower. C, D, side view of gynostegium. E, face view of gynostegium. F, papillae inside corolla outside mouth of 'primary' tube. G, pollinarium. Scale bars: A, B, 5 mm (at A); C, D, E, 1 mm (at A); F, 0.5 mm (at A); G, 0.25 mm (at A). Drawn from: A, B, D, F, PVB 4084, Okonguati, Namibia; C, E, G, Leistner et al. 19, 6 km south-west of Ruacana Falls, Namibia.

HOODIA PARVIFLORA



Fig. 4.88. *H. parviflora*, PVB 5587, near Okombambi, west of the Baynes Mountains, Namibia. Plant growing in a valley among trees of *Colophospermum mopane*, February 1993.



Fig. 4.89. *H. parviflora*, PVB 5587, near Okombambi, west of the Baynes Mountains, Namibia.

Diagnostic features and relationships

Plants of *H. parviflora* reach a remarkable size and specimens slightly over 2 m tall are not uncommon, making this the largest of all stapeliads and enabling it even to qualify as a tree. The considerable size of specimens might lead one to speculate that they reach a great age. They occur, however, in a region which is very hot but is not especially dry (receiving an annual average rainfall of probably 300 mm) and it appeared that plants could increase anything from 150 to 300 mm or more in a single season if reasonable rains fell. Thus a height of 1 m could easily be attained within five years if rains were reliable.

Hoodia parviflora is distinctive and easily recognised. The stems are thicker and taller than in any other species and have exceedingly long, uninterrupted rows of tubercles. This suggests that flowering only takes place after a certain, in some cases quite considerable, height has been reached. The epidermis has a characteristic matt bluish hue and is only greenish in the apical bud.

Hoodia parviflora has an unusual flowering time and flowers have usually been reported in June, July and August which, where it grows, is the beginning of the driest part of the year. However, plants were also seen flowering in February 1993, so that flowering does not take place only during the cooler months of winter.

In *H. parviflora* the pedicels are markedly shorter than normal and especially thick for the small size of the flowers. The corolla is usually between 30 and 55 mm across and so is relatively small. It has an unusual yellow to pale orange colour, usually with a reddish ring around the mouth of the tube and fairly impressed veins on the lobes and on the outer, tubular part. Generally the flower is funnel-shaped below the lobes and there is a small, cupular tube in the centre whose mouth is quite conspicuously thickened and pentagonal. The whole of the inside is finely bristly, each bristle arising from a small papilla, and these bristles generally have the same colour as the flower.



Fig. 4.90. *H. parviflora*, a particularly healthy specimen growing and flowering in the military base at Okonguati, Namibia, January 1990.

Right in the centre and somewhat hidden in the tube is the purple-black gynostegium. This is very similar to what one finds in *H. currorii*, with erect outer lobes with incurved margins which form a cup around the anthers. The gynostegium always seems to be slightly shorter than the tube.

The follicles in *H. parviflora* are unusual for the presence of a ridge running longitudinally along each edge which gives them a slightly angled appearance. In the field, seed is reported to develop quickly after flowering so that some seeds are already released before the first rains of late October to November (Tribe, pers. comm. 2000). However, maturing pods were also observed in the middle of January 1990 and in February 1993 so that this timing does not seem to be rigidly adhered to.

History

Hoodia parviflora was discovered by the Austrian biologist Friedrich Welwitsch who was commissioned by the government of Portugal to conduct botanical exploration in the colony of Angola. Welwitsch arrived in Luanda in September 1853 and returned to Portugal in 1861 (Hiem 1896-1901) and he met up with *H. parviflora* west of the Chela Mountains on 23 August 1859. He encountered it in several places and this enormous stapeliad, with stems 4-7 feet tall and *Cereus*-like appearance (Hiem 1896-1901) must have been scarcely less amazing than the extraordinary gymnosperm, later named *Welwitschia*, which he had found shortly before. *H. parviflora* was collected again in August 1899 by H. Baum somewhat closer to the Kunene River in Angola. Only much later did it become known in Namibia. Here it seems that the first specimens were recorded in 1959 by S. Triebner, who had found them while working in the Kaokoveld.

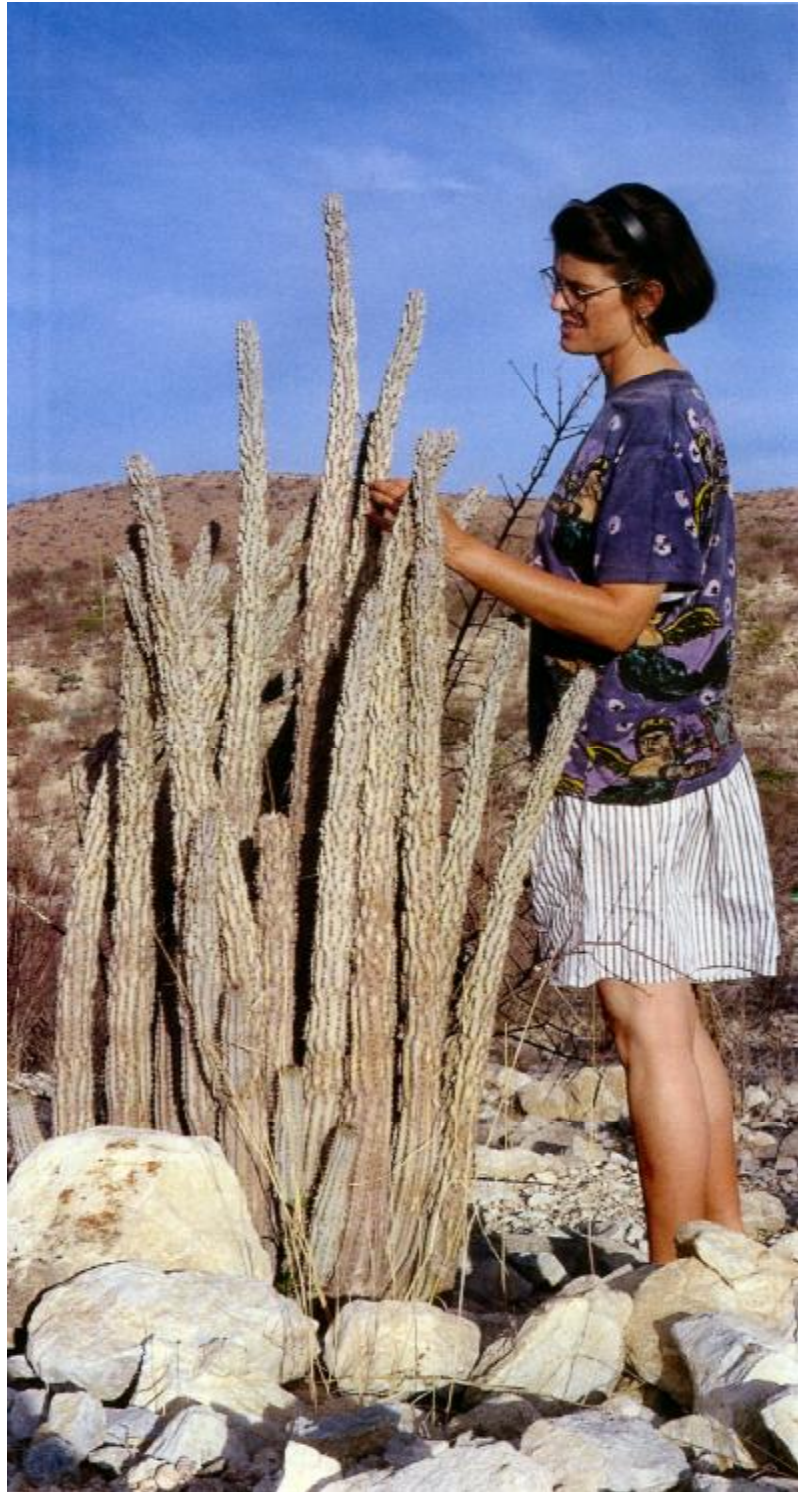
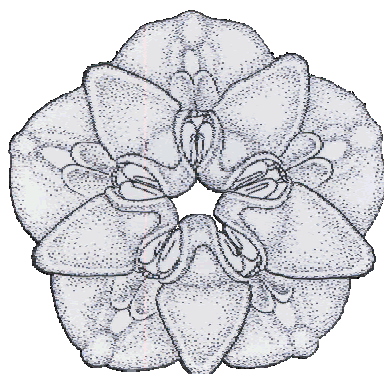


Fig. 4.91. *H. parviflora*, east of Epupa Falls, Namibia. Margaret Woermann scrutinizing a large plant slightly over 2 m tall, February 1993.

5. Huernia



Huernia was described by Robert Brown in 1810 and in this genus he included *Stapelia campanulata*, *S. guttata* and *S. venusta* of Masson. He characterised the genus by its apparently 10-lobed corolla, an effect which is caused by the five lobes of the corolla alternating with five smaller intermediate 'lobes' formed by folds of tissue between the bases of adjacent lobes. Brown did not formally transfer these species to his new genus; this was done by Haworth, who also moved more of Masson's species to *Huernia*. Haworth then included in *Huernia* both quite deeply tubular-flowered plants and others with a flatter flower with a prominent, shiny annulus. N.E. Brown (1890) still mentioned these intermediate corolla lobes in his key (p. 7) but added as well that in *Huernia* the outer corona is sessile and adnate to the base of the corolla. White & Sloane (1937) listed 45 species of *Huernia* but did not discuss its relationships with other genera. With the discovery of more species, the distinctions between *Huernia* and *Duvalia* became unclear and Leach (1969a; 1974a) expended considerable effort to sort this out. Despite his efforts, it remains true that *Duvalia* and *Huernia* are difficult to distinguish morphologically and the problems involved here are discussed in detail under *Duvalia*. Nevertheless, these two genera are distinguished from most other stapeliads by several characters that have only recently come to light (Bruyns 2000a).

In *Huernia* White & Sloane (1937) recognised 45 species (divided into five 'groups') while Leach (1988) recognised 64, which he subdivided into a complicated arrangement of sections, subsections, series and subseries. These were built from the two sections recognised by K. Schumann (1895), which had been extended to four sections by A. Berger (1910). A further five species have been described subsequent to Leach's revision (Newton & Lavranos 1993; Plowes 1995a; Plowes & McCoy 2002; Plowes 2003a). Many of the names described after 1937 are for new taxa discovered in Africa north of the equator and from Arabia. However, Leach's figure is definitely too high. Some synonymy

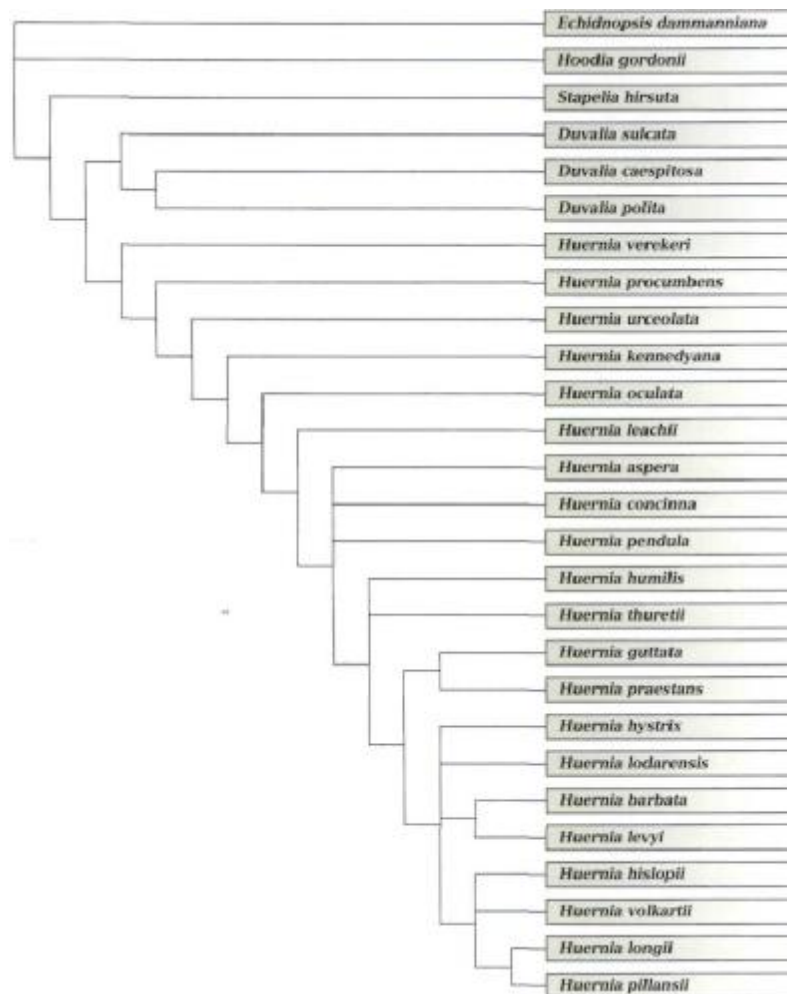


Fig. 5.1. Simplified cladogram derived from morphological characters showing the possible relationships among the species of *Huernia*.

can be deduced from the evidence presented by Leach (1988) and from material preserved in Zürich (at ZSS). *Huernia schneideriana* is almost certainly a hybrid that was collected only once (Leach 1969a) and there is therefore no reason to treat this as a species. This brings the number of species in north-eastern Africa and Arabia down to 14 as follows:

H. archeri L.C.Leach
H. aspera N.E.Br. (including *H. keniensis* R.E.Fries,
H. lenewtonii Plowes)
H. concinna N.E.Br. (including *H. formosa* L.C.Leach and *H. lavrani* L.C.Leach)
H. erinacea P.R.O.Bally
H. hadramautica Lavranos (including *H. rubra* Plowes)
H. laevis J.R.I.Wood

H. lodarensis Lavranos (including *H. khalid-binsuitanii* Plowes & McCoy, *H. nigeriana* Lavranos, *H. boleana* M.Gilbert and *H. saudi-arabica* D.V.Field)

H. maccoyii Plowes

H. marnieriana Lavranos

H. penzigii N.E. Br (including *H. arabica* N.E.Br.)

H. recondita M.Gilbert

H. rosea Newton & Lavranos

H. somaiica N.E.Br.

H. tanganyikensis (Bruce & P.R.O.Bally)
L.C.Leach (including *H. andreana* Rauh)

In southern Africa, the number of species is reduced here to 33. Two species, *H. erectiloba* (central and northern Mozambique) and *H. similis* (northern Angola) occur outside these

areas (though the former is included in this account), so that a total of 34 species is treated in this account. Evidence suggests therefore that *Huernia* has a total of 49 species and this makes it the third largest genus in the stapeliads after *Caralluma* and *Orbea*.

Huernia R.Br., *Asclepiadeae*: 11 (1810) as '*Heurnia*' in G. Don, *Gen. Hist.* 4:112 (1837-8).

Huernia sect. *Orthostelma* K.Schum. in Engl., *Pflanzenfam.* 4 (2): 280 (1895), nom. superfl. Lectotype: *Huernia campanulata* (Masson) Haw. [= *Huernia barbata* (Masson) Haw.].

Decodontia Haw., *Syn. Pl. Succ.* 28 (1812), nom. nud.

Huernia sect. *Huernia* subsect. *Calostelmae* (A.Berger) L.C.Leach, *Excelsa Taxon.* Ser. 4: 9 (1988).

Huernia sect. *Huernia* subsect. *Calostelmae* ser. *Multangulares* L.C.Leach, *Excelsa Taxon.* Ser. 4:9 (1988).

Huernia sect. *Calostelma* A.Berger, *Stap. u. Klein.*: 137 (1910).

Lectotype: *Huernia pillansii* N.E.Br.

Huernia sect. *Huernia* subsect. *Calostelmae* ser. *Pauciangulosae* subser. *Podostelmae* (A.Berger) L.C.Leach, *Excelsa Taxon.* Ser. 4:10 (1988).

Huernia sect. *Podostelma* A.Berger, *Stap. u. Klein.*: 137 (1910).

Lectotype: *Huernia hystrix* (Hook. f.) N.E.Br.

Huernia sect. *Huernia* subsect. *Huernia* ser. *Annu-
iatae* L.C.Leach, *Excelsa Taxon.* Ser. 4: 9 (1988).
Type: *Huernia guttata* (Masson) Haw.

Huernia sect. *Huernia* subsect. *Calostelmae* ser. *Pauciangulosae* L.C.Leach, *Excelsa Taxon.* Ser. 4:10 (1988).

Huernia sect. *Huernia* subsect. *Calostelmae* ser. *Pauciangulosae* subser. *Austerales* L.C.Leach, *Excelsa Taxon.* Ser. 4:10 (1988).
Type: *Huernia longituba* N.E.Br.

Huernia sect. *Huernia* subsect. *Calostelmae* ser. *Pauciangulosae* subser. *Boreales* L.C.Leach, *Excelsa Taxon.* Ser. 4:10 (1988).
Type: *Huernia erinacea* P.R.O.Bally.

Huernia sect. *Plagiostelma* K.Schum. in Engl., *Pflanzenfam.* 4 (2): 280 (1895).

Huernia sect. *Plagiostelma* ser. *Asperae* L.C.Leach, *Excelsa Taxon.* Ser. 4:11 (1988).
Lectotype: *Huernia aspera* N.E.Br.

Huernia sect. *Plagiostelma* ser. *Asperae* subser. *Urceolatae* L.C.Leach, *Excelsa Taxon.* Ser. 4:11 (1988).

Type: *Huernia urceolata* L.C.Leach.

Huernia sect. *Plagiostelma* ser. *Humiles* L.C.Leach, *Excelsa Taxon.* Ser. 4:11 (1988).
Type: *Huernia humilis* (Masson) Haw.

Huernia sect. *Plagiostelma* ser. *Humiles* subser. *Convexae* L.C.Leach, *Excelsa Taxon.* Ser. 4:11 (1988).

Type: *Huernia somaica* N.E.Br.

Huernia sect. *Plagiostelma* ser. *Ampligibbae*

L.C.Leach, *Excelsa Taxon.* Ser. 4:11 (1988).

Huernia sect. *Plagiostelma* ser. *Ampligibbae* subser. *Verekeriae* L.C.Leach, *Excelsa Taxon.* Ser. 4:11 (1988).

Type: *Huernia verekeri* Stent.

Huernia sect. *Plagiostelma* ser. *Ampligibbae* subser. *Procumbentes* L.C.Leach, *Excelsa Taxon.* Ser. 4: 12 (1988).

Type: *Huernia procumbens* (R.A.Dyer) L.C.Leach.

Huernia sect. *Plagiostelma* ser. *Cleistostelmae* L.C.Leach, *Excelsa Taxon.* Ser. 4:12 (1988).

Type: *Huernia lavrani* L.C.Leach [= *Huernia concinna* N.E.Br.].

Huernia sect. *Fallacistelma* L.C.Leach, *Excelsa Taxon.* Ser. 4: 12 (1988).

Type: *Huernia brevirostris* N.E.Br. [= *Huernia thuretii* F.Cels.]

Spineless rarely rhizomatous (*H. longii* only) succulent mostly forming compact clumps or dense mats, sometimes prostrate and creeping, or somewhat pendulous (from ledges on cliffs). Stems 10-150 (-500) mm long, 5-25 mm thick, erect, decumbent or prostrate, fleshy and firm, glabrous, mostly grey-green sometimes mottled with purple or red; tubercles 1-15 mm long (including leaf-rudiment), deltoid to conical, spreading, sometimes laterally flattened, joined into 4-16 sometimes spiralling angles along stem (sometimes prominently wing-like, sometimes only low ridges), each tipped with a soft (rarely spike-like or bristle-like) acute to acuminate leaf-rudiment, without stipular denticles. Inflorescence glabrous, usually only 1 per stem, arising mainly in lower half of stem, each bearing 1-10 flowers developing in gradual (rarely quick) succession from short peduncle (mostly < 5 mm long), with several lanceolate to filiform bracts (1-) 2-8 mm long without lateral teeth; pedicel (2-) 10-30 (-60) mm long, 1.0-2.5 mm thick, ascending to spreading; sepals (3-) 4-12 (-15) mm long, 1-2 mm broad at base, acuminate. Corolla (8-) 20-70 mm diam., tubular (urceolate) to campanulate to subrotate, sometimes strongly reflexed (and slightly thickened) below bases of lobes to form prominent annulus around mouth of tube, mostly shallowly lobed; outside glabrous, smooth to papillate, with 1-5 raised longitudinal veins on lobes; inside mostly with conical to dorsiventrally flattened obtuse multicellular papillae especially around mouth of tube with an often much elongated inflated apical bristle, rarely smooth, never transversely rugulose; tube usually at least 5 mm deep, cupular (rarely shallowly bowl-shaped), cylindrical to pentagonal; lobes (2-) 6-18 mm long, 4-17 mm broad at base, spreading to reflexed, deltate, acute to acuminate, usually flat to concave above, margins without cilia. Corona (2-) 3-9 mm tall, (2.5-) 3.5-8 mm broad, consisting of 2 series arising on staminal tube and well separated from each other, glabrous, sessile and often somewhat fused to base of tube beneath outer lobes (with very slight stipe in *H. oculata*, *H. procumbens*, *H. urceolata*, *H. verekeri* and longer one in *H. kennedyana*); outer lobes spreading along base of tube, discrete (and often shallowly bifid) to fused into spreading disc, with fleshy tubercle beneath guide-rail obscuring entrance to small nectarial cavity (absent in *H. procumbens* and in *H. verekeri* and

sometimes in *H. oculata*); inner lobes adpressed to backs of anthers at least in lower half of anthers, mostly exceeding them and meeting in centre or rising up connivent and then diverging, dorsiventrally flattened towards base but becoming terete above and slender to clavate at often bristly apex, at base with rounded spreading (rarely ± erect) transverse dorsal gibbosity or ridge. Anthers horizontal on top of style-head, margins shrinking back to expose pollinia, rectangular. Pollinium ellipsoidal, longer than broad, insertion-crest exactly along outer edge, caudicle attached with broad cupular pad to base. Follicles erect, terete-fusiform, obclavate, slender, consisting of 2 horns diverging at 30-60°, longitudinally mottled with narrow broken purple stripes, glabrous, smooth.

Most plants of *Huernia* form relatively dense clumps with the stems erect from a short, horizontal base. In a single species, *H. longii* from the Eastern Cape in South Africa, the stems are rhizomatous. As is usual in such cases, the plant has a small to large central clump of more or less erect stems with the others spreading away from this clump horizontally beneath the surface, emerging at intervals of up to 300 mm or more away from the main plant. There are several species (*H. leachii*, *H. pendula*, *H. procumbens* and *H. tanganyikensis*) where the stems are wholly prostrate. These are all found along the eastern flank of Africa, from the Eastern Cape (in the former Transkei) through Mozambique to around Mt Kilimanjaro. Two species (*H. verekeri* and *H. volkartii*) have varieties or subspecies with this habit whereas the typical varieties (or subspecies) have more erect stems. In one case (*H. pendula*), these stems may be pendulous from ledges on cliffs but in most others they creep on rocks amongst leaf-litter in somewhat shady habitats in hilly to mountainous terrain. Such creeping stems from dense to diffuse mats in which individual stems may reach 500 mm or longer and they are invariably almost cylindrical with hardly any angles.

The number of angles into which the tubercles are arranged along the stems is extremely variable across the genus, especially among the southern African species. Most species have 4-5 angles but 6-angled stems can often be found and are common in *H. verekeri*. Three species, *H. kennedyana*, *H. longii* and *H. pillansii*, have more angles: 7-9 in *H. kennedyana*, 6-9 in *H. longii* and 10-16 in *H. pillansii*. In all of these the stems have a cylindrical to nearly spherical and distinctly tessellate shape and are quite unlike those of other *Huernias*.

The stems are always glabrous and smooth. Mostly they are uniformly coloured, although mottling with dark purple is found in several north-eastern African and Arabian species and a few in southern Africa (e.g. in *H. guttata* and *H. erectiloba*). Tubercles on the stems are variable in shape and in the extent to which they are vertically joined. In some they are

strongly laterally flattened and longitudinally joined into prominent, thin wings along the stem whereas in others they are conical and joined into only low angles; the angles are especially low in the prostrate-stemmed species. Each tubercle tapers gradually into a leaf-rudiment. This is always small, though often quite slender, and exhibits no distinct structure (midrib, blade, petiole, etc.) apart from being slightly broader towards the base. It is also always slightly flattened above and has no trace of stipular denticles around its base. It becomes hardened, yellow and thorn-like in *H. hystrix* (and to a lesser degree in *H. nouhuysii*) but is usually soft and gradually wears off. In *H. pillansii* it is a soft, slender bristle.

Inflorescences in *Huernia* arise mainly in the lower half of the stem, with only one per stem. They are fairly variable in size and in the number of flowers that they bear, though the peduncle remains short. Simultaneously opening clusters are never produced, although in a few (notably *H. blyderiverensis*, *H. nouhuysii* and *H. quinta*, where particularly large numbers of flowers are produced on each inflorescence) the flowers open in rapid succession or several may be open on an inflorescence at once. The bracts in the inflorescence are often long and slender and always lack the lateral teeth that are often found in other genera. The sepals may also be unusually long and slender and can exceed the length of the corolla tube.

The corolla in *Huernia* exhibits a particularly wide range of shapes. It may be almost entirely flat in the Arabian *H. marnieriana* and in southern Africa the nearest to this is found in *H. leachii* or *H. oculata*, where it forms a small, relatively shallow bowl. In species such as *H. thuretii* and *H. nouhuysii* there is a cup-shaped tube in the centre with the lobes spreading perpendicular to its mouth and forming a flat area around the mouth. More trumpet-shaped to cylindrical corollas are found in *H. barbata* and *H. longituba* and this shape reaches an extreme in *H. levyi* which has the longest corolla tube of any *Huernia*. Perhaps the most unusual form in the corolla is the nearly spherical tube with small lobes spreading around its mouth which is found in *H. urceolata*. In most species the lobes are shorter than the central, united part of the corolla but the reverse is the case in *H. procumbens* and *H. verekeri*, where the lobes are long and slender and greatly exceed the diameter of the short tube and central area. The edges of the corolla lobes are usually folded upwards so that, at least towards their tips, they are mostly concave or slightly channeled above.

The annulus in the corolla reaches its most prominent form in such species as *H. guttata*, *H. procumbens*, *H. somaica*, *H. zebrina* and others. If the flower of, say *H. zebrina*, is turned over and viewed from the rear, it will be found that the corolla rises up around the corona to form

a tube and then is abruptly bent back towards the pedicel a little below the bases of the lobes, with the lobes then spreading from a lower level than the mouth of the tube. From the back of the flower, the area around the mouth of the tube appears to have a distinct, sunken ring in it (which can be seen in the bud, though only just before it matures). From the front of the flower the mouth of the tube is surrounded by a prominent, shiny annulus. If the flower is dissected (fig. 24 B), it is found that the corolla reaches a maximum of 2-4 times as thick in the annulus as below it, while in some species (such as *H. procumbens*) it is not thickened at all around the mouth of the tube. Therefore the prominence of the annulus and the mouth of the tube is caused largely by the manner in which the corolla is bent back above the mouth and not especially by the thickness of the annulus itself. The corolla tube is also then not a consequence of a massively thickened annulus in an otherwise nearly flat corolla as is the case, for example, in all species of *Duvalia*.

In several species which do not have a prominent annulus, traces of it exist in the form of a distinct thickening in the tube accompanied by changes in the distribution of papillae around it as, for example, in *H. hislopilii* (fig. 24 E), *H. levyi* and *H. occulta*. In such species as *H. hislopilii*, *H. levyi* and *H. occulta*, the presence of these traces of an annulus deep within the corolla tube suggests that the lower part of this tube corresponds to the 'primary' tube and the remainder of the corolla tube as well as the often saucer-like area beyond its mouth correspond to the 'secondary' tube. This makes for interesting comparison with *Hoodia*, where a similar situation exists and the corolla tube is also made up of two distinct parts. In other taxa (especially in the southern Cape) there is a gradual transition from flowers with a prominent annulus (e.g. *H. humilis*) to flowers where it is much less prominent (some specimens of *H. humilis*, *H. praestans*, some forms of *H. thuretii*) and further to flowers which are scarcely thickened at all around the mouth of the tube (other forms of *H. thuretii*). In many of the southern African species, the annulus is completely absent.

Papillae are found very widely both on the outside and on the inside of the corolla in *Huernia*. In several species the outside of the corolla is distinctly rough with small, rounded papillae. In all cases examined, these papillae turned out to be raised stomata and such structures are also known in flowers of some species of *Ophionella* and *Pectinaria* (fig. 25 C). In almost all species of *Huernia* the inside of the corolla is papillate, being smooth only in *H. urceolata*. These papillae consist of a multicellular, cylindrical to conical base with a more or less obtuse apex whose apical cell is elongated into a variously shaped bristle. In some the base is prominent (up to 3 mm long

in *H. kennedyana* and generally this is more so in tropical to subtropical species) and the apical cell is a minute bristle. In others the basal zone is short (sometimes even almost absent) and the apical bristle is up to 5 mm long (e.g. *H. guttata*). This apical cell takes on a remarkable array of shapes when the base is short and may be found from slender and bristle-like to cylindrical to variously clavate or even, in some cases, nearly spherical. Some idea of the range of shapes in these structures can be obtained from fig. 28.

In most species, particularly in southern Africa but also in the northern part of the distribution, the gynostegium is very similar. It has widely been assumed to be sessile (Leach 1969a, 1974a, Meve 1997) and this is indeed mostly the case. However, in a few species (*H. oculata*, *H. urceolata* and *H. procumbens*) there is a very short stipe that raises the outer corona slightly above the base of the tube; in *H. kennedyana* it is raised quite significantly. The outer corona lobes are always finely papillate and are mostly more or less rectangular, spreading on the base of the tube and frequently partially fused to it (sometimes almost to their tips). Very occasionally they are fused into a slightly dish-like disc. Towards their bases they become fused into a plate around the gynostegium which rises towards the bases of the guide-rails. In most species there is a small, erect tubercle just below the rails, which stands in front of and obscures the mouth of the nectarial cavity. The outer lobes may sometimes be very much reduced (see *H. hallii* and *H. oculata*) so as to form a small, steeply sloping disc whose edges are pressed to the base of the tube.

Well above the level of the outer coronal disc, the inner lobes begin at the backs of the anthers. They are always adpressed to the anthers and sometimes rise in the centre. Towards their bases they are dorsiventrally flattened but above they often become cylindrical and their apices may be papillate or even variously swollen (as can be seen in *H. hystrix*). At their base, each has a transverse, dorsal ridge or swelling (except in *H. concinna* and *H. urceolata*). In some species small, sweat-like droplets of nectar are secreted on the inner lobes.

One of the most obvious features of these coronal structures is the considerable separation that has taken place between the outer series at the base of the corolla tube and the inner series arising at the bases of the anthers. This separation is even more obvious in *Huernia* than in *Duvalia*. In *Huernia* the outer corona begins to develop before the inner. Almost immediately, this meristem starts to form a ridge of tissue running upwards between adjacent guide-rails to the base of the anther where, a little later, the inner corona begins to form. This ridge of tissue between the guide-rails, which probably also constitutes part of the

HUERNIA

outer coronal series, swells up with time to join the lower part of the outer corona to the bases of the inner lobes. It does not develop in *Duvalia* but has been observed in species such as *H. procumbens* and *H. verekeri* where the corona is otherwise somewhat 'Duvalia-like'.

Among the tropical species there are several where the gynostegium has a rather different appearance to that normally associated with *Huernia*. In particular, this is the case in *H. concinna*, *H. procumbens*, *H. tanganyikensis*, *H. urceolata* and *H. verekeri*. In *H. concinna* and *H. urceolata* this is brought about by the staminal tube being far shorter and thicker below the anthers than is usual in *Huernia*. Both species also have unusually broad inner corona lobes which virtually cover the top of the gynostegium or, in *H. concinna*, hide the anthers completely. In *H. procumbens*, *H. tanganyikensis* and *H. verekeri* the staminal tube is also shorter but is not so thick. Here there is also a dramatic increase in the size of the dorsal projection on the inner corona lobes and this entirely dwarfs the real inner lobes. In such cases the whole structure resembles that in *Duvalia* rather than those typical of *Huernia*.

The presence of a small tubercle on the outer corona just below each guide-rail has already been mentioned. This is finely papillate just like the rest of the outer corona. Half-flowers indicate that it is the usual lip of the outer corona which normally encloses the mouth of the nectarial cavity and here, instead of remaining flush with the surface and pointing towards the base of the guide-rail, it stands up vertically and so projects somewhat out of the surface of the gynostegium. It is, therefore, not a new structure. The nectarial cavity behind this lip is laterally very shallow. It varies very much in depth; for example, the lip is quite tall in *H. zebrina* but is small, with a small cavity, in *H. urceolata*. The lip is absent in *H. procumbens* and so the tubercle is absent and here the nectarial cavity is simply an almost horizontal bay below the rails. In *H. verekeri* and sometimes in *H. oculata* there is no tubercle beneath the guide-rail but there is still a small lip enclosing the cavity. This slopes inwards as in most other stapeliads, which is why the tubercle is absent.

The pollinaria of *Huernia* (fig. 32 B shows a typical example) are very similar to those of *Duvalia*. Here the pollinia are ellipsoidal with a thick insertion-crest along the outer edge (the crest is always a little longer than that in *Duvalia*) and a short, broad corpuscle with relatively short, acute lateral wings (these are much longer and usually obtuse in *Duvalia*). The caudicle has a broad, almost cupular patch which is attached to the 'base' of the Pollinium.

Seeds in *Huernia* are mostly broad and almost circular in outline, with usually distinctly thickened and considerably inflated,

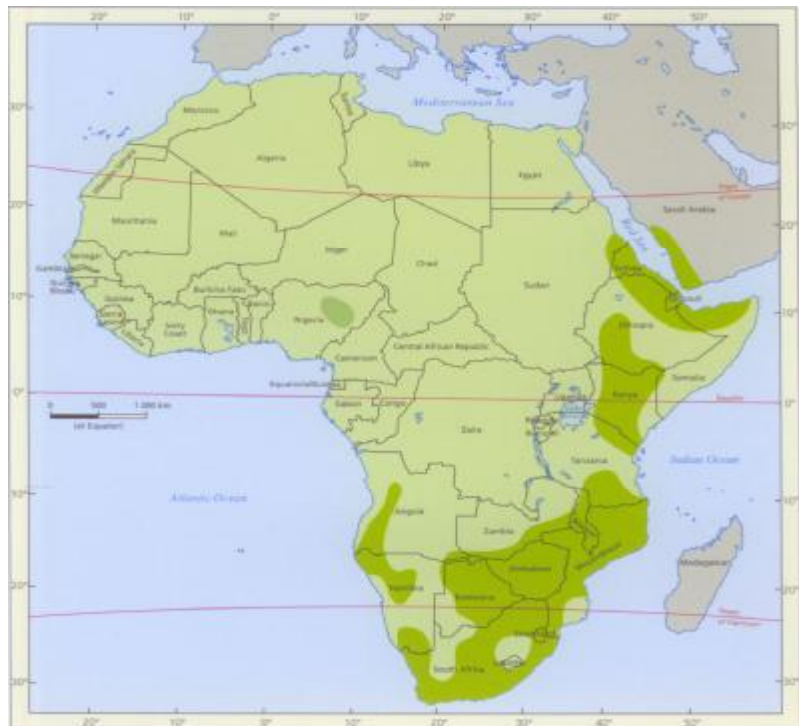


Fig. 5.2. Distribution of *Huernia*.

often rather shiny margins. However, in *H. kennedyana*, *H. pendula* and *H. verekeri* the seed is narrowly pear-shaped in outline and has a thin margin. The seedlings have a wedge-shaped hypocotyl that is often quite broad and bears narrow and undifferentiated cotyledons spreading horizontally at the apex.

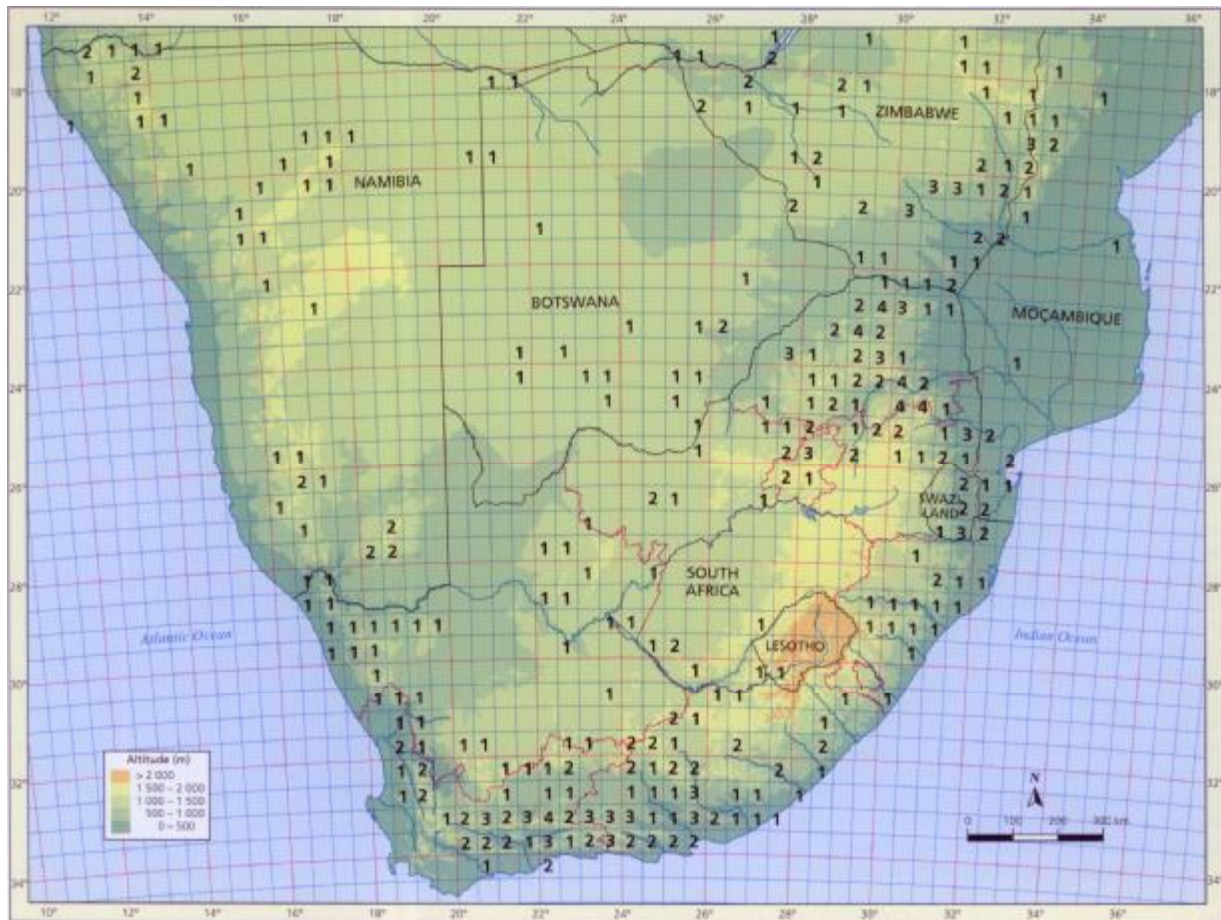
Huernia species occur in the south-western corner of Arabia (in the Yemen and in Saudi Arabia) and on the adjacent opposite side of the Red Sea from eastern Sudan through Ethiopia to northern Somalia (fig. 5.2). A little further south they occur in southern Ethiopia, Kenya and as far as central Tanzania. Further south of this there appears to be a gap, after which *Huernia* is found again sporadically in Malawi and southern Zambia. Yet further south *Huernia* occurs widely in Zimbabwe, Botswana, Mozambique and in South Africa as far as 34°S. The genus is not found in the high-lying parts of Lesotho and in the adjoining region of the Free State, and is also absent in some parts of Mozambique.

There is an apparently disjunct area where *Huernia* occurs in northern Namibia, with a narrow tongue extending into Angola.

This disjunction is also found in *Stapelia*. A further, remarkable disjunct patch occurs in

the highlands of central Nigeria. The 'species' that occurs here, *H. nigeriana* Lavranos, was once thought to be part of *H. volkartii* (Lavranos 1964), which has its nearest known locality in northern Angola. Leach (1976a; 1988) showed, though, that these plants were more similar to the complex surrounding *H. lodarensis* and they almost certainly represent a western outpost of this species. Such east-west disjunction in species of stapeliads is also known in *Caralluma adscendens*, *C. edulis*, *C. acutangula* and *Orbea decaisneana*, and a similar pattern of disjunction has been observed in *Aloe* (Holland 1978). The disjunction between West Africa and the remainder of the distribution is certainly real and similar ones are known in *Brachystelma* (Meve & Porembski 1993) and perhaps in *Neoschumannia* (Meve 1995a). However, some of the disjunctions on the eastern flank of the continent may be a consequence of inadequate collecting.

Within South Africa, where the distribution is known in more detail than anywhere else, it shows several peculiarities (fig. 5.3). As in *Stapelia*, there are widely distributed and localised species and, as in that genus, the localised species are almost always found in mountainous areas. The largest number of



species per half-degree square is four, found in the Soutpansberg (2 local, 2 widely distributed species), Eastern Transvaal (1 local, 3 wider) and in the mountainous parts of the Little Karoo where species from the west and species from the east meet up (none of them especially local). Species are absent from the driest parts of the Namib (though see the distribution of *H. oculata* for an exception), from much of the sandy, eastern parts of Namibia and western Botswana, from the very calcareous, low-lying area in north-eastern Botswana and from the highest parts of the Drakensberg. They are also absent from the south-western Cape around the Cape Peninsula and the Worcester-Robertson Karoo. There is one species, *H. longituba*, which has somewhat of a broad, central distribution such as in *D. polita*, but it is not as widely distributed as many others with this kind of distribution.

Leach (1988) pointed out some unusual patterns of disjunction in the distribution of some species of *Huernia*. Possibly the most extreme

example that he gave is of *H. volkartii*, which occurs in Angola and Zimbabwe, separated by a distance of approximately 1 800 km and this again has parallels in *Aloe* (Holland 1978). Another remarkable case is that of *H. thuretii*, which grows along the coastal area of the Eastern Cape and has also been recorded in a small area in the Tiras Mountains north of Aus in southern Namibia, nearly 1 000 km away. Leach (1988) also mentioned the peculiarly disjointed distribution of *H. zebrina* which is common in northern South Africa but to the west occurs in an isolated patch around Serowe in Botswana and in two widely separated spots in Namibia. Another example is provided by the very localised *H. pendula* from the Eastern Cape. Its closest relative is apparently *H. similis*, which is only known in the mountains of northern Angola and is again very local. When complexes of very closely allied species are considered, these unusual patterns become more emphasised. In both the '*brevistrois*' complex (here Leach (1988) recognised *H. bayeri*, *H. bre-*

virostris, *H. hallii*, *H. namaquensis*, *H. nouhuysii*, *H. quinta* and *H. thuretii*) and the '*zebrina*' complex (*H. zebrina*, *H. insigniflora*, *H. plowesii*, *H. humilis* and *H. thudichumii* of Leach (1988)), taxa occur in isolated patches which are found in the central or Eastern Cape, north-eastern South Africa and in the mountains of southern Namibia and Namaqualand. A somewhat similar picture emerges in the '*guttata*' complex (*H. erectiloba*, *H. guttata*, *H. reticulata* and *H. transvaalensis* of Leach (1988)), though here one member (*H. erectiloba*) occurs as far afield as northern Mozambique. In both the '*guttata*' and the '*zebrina*' complexes one finds plants with transversely striped flowers in the northern part of the distribution and ones with spotted flowers in the southern part and this pattern is partly repeated in the '*brevistrois*' complex. It is not clear to what extent the dispersal of the seed is responsible for these distributions or to what degree they might be relictual.

Key to the species

1. Inner corona lobes much exceeding anthers 2
2. Inner corona lobes tapering to a fine point 3
3. Corolla without broad annulus around mouth of tube 4
4. Corolla inside with papillae tipped with spherical to clavate or long and slender bristle (up to 3 mm long) at least in mouth of tube, longest of bristles much longer than papillae on which they arise 5
5. Corolla tubular-campanulate to bicampanulate, corolla tube at least as long as broad 17. *H. barbata*
5. Corolla almost rotate, with shallow tube somewhat broader than long 18. *H. piersii*
4. Corolla inside with papillae usually tipped with short acute bristle, longest of bristles almost equalling papillae on which they arise (usually shorter than them) 8. *H. thuretii*
3. Corolla with broad (often shiny) annulus around mouth of tube 6
6. Inside of corolla with conspicuous papillae (each with apical bristle) only around and below mouth of tube (rarely on annulus as well) 7
7. Corolla lobes inside transversely lined with red to maroon on cream to yellowish, inner corona lobes only slightly divergent towards tips 20. *H. transvaalensis*
7. Corolla lobes inside with round and not transversely elongated dark spots, inner corona lobes strongly divergent in upper half 8
8. Corolla tube mostly broader than long, without constriction in middle 19. *H. guttata*
8. Corolla tube longer than broad, with constriction around middle 21. *H. erectiloba*
6. Inside of corolla with conspicuous papillae (each with apical bristle) from below mouth of tube onto annulus and on lobes 22. *H. praestans*
2. Inner corona lobes not tapering to a fine point 9
9. Stems with 6 or more angles 10
10. Stems mostly spherical, corolla with shallowly cupular tube, inside cream to dull yellow and irregularly transversely lined with red-brown to dark maroon, inner corona yellow 7. *H. kennedyana*
10. Stems mostly cylindrical, corolla with cupular tube at least as deep as broad, inside cream to brownish marked densely with fine red-brown spots, inner corona red to maroon 11
11. Stems (9-) 10-16 (-24)-angled, each tubercle tipped with a slender soft bristle 2-8 mm long, corolla lobes 12-22 mm long 33. *H. pillansii*
11. Stems 8-9-angled, each tubercle tipped with a short lanceolate tooth 1-2 mm long, corolla lobes 5.0-10.5 mm long 34. *H. longii*
9. Stems 4-5-angled (5-angled only rarely) 12
12. Inner corona lobes distinctly swollen towards apex, regularly clavate to somewhat inverted foot- or hoof-like 13
13. Corolla tube broader than long 14
14. Inner corona lobes apically much swollen into inverted foot-like or hoof-like structure, not bristly around apex, pedicel at least 15 mm long 23. *H. hystrix*
14. Apices of inner corona lobes not greatly swollen but noticeably bristly, pedicel mostly < 12 mm long 15
15. Stems 4-angled (5-angled only rarely) 16
15. Corolla lobes > 1.5 times as long as broad 30. *H. stapelioides*
15. Corolla lobes = as long as broad 31. *H. loeseneriana*
15. Stems 5-angled (4-angled only rarely) 29. *H. volkartii*
13. Corolla tube longer than broad 17
17. Corolla tube and papillae inside corolla dark maroon, corolla bicampanulate 25. *H. kirkii*
17. Corolla tube concentrically dark-lined on pale background inside, papillae inside corolla spotted and banded, corolla tubular-campanulate 26. *H. longituba*
12. Inner corona lobes very slightly or not at all swollen at apex (not as above) 18
18. Inner corona lobes narrowing towards apices 19
19. Corolla at least 40 mm in diameter 20
20. Corolla campanulate, with relatively long tube widening towards lobes, inner corona lobes arising well above outer lobes 24. *H. hislopil*
20. Corolla bicampanulate, with relatively short tube abruptly widening at its mouth, inner corona lobes arising close to outer lobes 27. *H. occulta*
19. Corolla at most 35 mm in diameter 21
21. Corolla widening gradually from base of tube to tips of lobes, longest papillae inside corolla at least 1 mm long and much taller than thick, inner corona lobes 2.5-4.0 mm long 32. *H. whitesloaneana*
21. Corolla usually abruptly flattened at mouth of tube, longest papillae inside corolla < 1 mm long (excluding apical bristle) and only slightly taller than thick, inner corona lobes at most 2.0 (-2.5) mm long 22
22. Flowers borne in dense clusters, often several opening at once on peduncle 11. *H. nouhuysii*
22. Flowers borne in small groups, opening in gradual succession 8. *H. thuretii*
18. Inner corona lobes + cylindrical and obtuse 28. *H. levyl*

(Continued on next page)

Key to the species (continued)	
1. Inner corona lobes at most shortly exceeding anthers	23.
23. Corolla globose-urceolate, inside without papillae, inner corona lobes uniformly swelling towards base and without transverse dorsal projection	3. <i>H. urceolata</i>
23. Corolla not globose-urceolate, inside finely to coarsely papillate (rarely smooth), inner corona lobes not uniformly turgid, with variably prominent rounded transverse dorsal projection	24.
24. Inner corona lobes with dorsal projection exceeding length of lobes	25.
25. Corolla with prominent annulus around mouth of tube, tube only slightly broader than corona	2. <i>H. procumbens</i>
25. Corolla without annulus, tube broadly saucer-shaped and much broader than corona	1. <i>H. verekeri</i>
24. Inner corona lobes with dorsal projection present only as small transverse swelling	26.
26. Corolla thickened around mouth of tube to form annulus	27.
27. Corolla lobes with broad transverse markings, if unmarked then annulus darker than rest	16. <i>H. zebrina</i>
27. Corolla lobes distinctly spotted, if unmarked then annulus pale cream	28.
28. Corolla tube strongly pentagonal, with scattered bristles around mouth	15. <i>H. plowesii</i>
28. Corolla tube cylindrical to at most slightly pentagonal, glabrous or rarely with few bristles around mouth	14. <i>H. humilis</i>
26. Corolla without any annular swelling around mouth of tube	29.
29. Stems slender and only obscurely angled, pendulous or creeping horizontally	30.
30. Leaf-rudiments absent, inside of corolla uniformly dark maroon	6. <i>H. pendula</i>
30. Leaf-rudiments fine and lanceolate, $\pm$ 2 mm long, inside of corolla cream with fine broken concentric lines	5. <i>H. leachii</i>
29. Stems clearly 4-5-angled, stout, erect and clump-forming	31.
31. Inside of corolla cream to white, variably spotted or lined	32.
32. Flowers borne in dense clusters, often several opening at once on peduncle	33.
33. Stems 4-angled, apical bristle on papillae inside corolla < 0.25 mm long	13. <i>H. blyderiverensis</i>
33. Stems 5-angled, apical bristle on papillae inside corolla up to 1 mm long	12. <i>H. quinta</i>
32. Flowers borne in small groups, opening in gradual succession	34.
34. Inner corona lobes 1.5-2.5 mm long, reddish to blackish	8. <i>H. thuretii</i>
34. Inner corona lobes 0.5-1.4 mm long, mostly yellow	35.
35. Papillae inside corolla up to 0.25 mm long	10. <i>H. hallii</i>
35. Papillae inside corolla up to 0.5 mm long	9. <i>H. namaquensis</i>
31. Inside of corolla deep maroon-black (rarely green) above, changing abruptly to contrasting white circular areas in lower half of tube	4. <i>H. oculata</i>

The relationships between the species were not elucidated by Leach (1988). He set up a complicated system of three sections, with two subsections, eight series and seven subseries but did not use them in his key nor did he investigate how they were related to one another. Of the eight species included in his section *Fal-lacistelma*, he said that they are 'more closely related to each other than to any other of the recognised groupings' and formed a 'natural group'. Nevertheless, he could not find any character which defined the section and this example demonstrates some of the problems in this arrangement. In particular, the fact that *H. procumbens*, *H. verekeri* and to a lesser extent *H. tanganyikensis* and *H. urceolata* share so many characters with *Duvalia* seemed to indicate that, within *Huernia*, they should be most closely related to the species of *Duvalia*.

In an attempt to clarify the relationships between the species, a cladistic analysis of morphological characters was carried out. The results of this analysis are shown as fig. 5.1. As a consequence of this analysis, no subdivisions of the genus are recognised. The arrangement of the species in this account is taken from the cladogram. Those species not employed in the analysis are placed adjacent to species that were used and to which they are

morphologically most similar.

Our molecular investigations (involving 11 species of *Huernia*, including *H. procumbens*) have shown that *Huernia* is a monophyletic entity separate from *Duvalia*, but their relationships are unresolved.

1. *Huernia verekeri*

Huernia verekeri Stent, Bull. Misc. Inform. 1933: 145 (1933).

Type: Zimbabwe, Sabi Valley, Vereker sub SRGH 5427 (K, nolo.; PRE, iso.).

Small succulent forming diffuse clump to 500 mm (±1 m) diam. Stems 30-100 mm long, 6-12 mm thick (excluding teeth), decumbent to prostrate, green to purplish green; tubercles 3-15 mm long, lanceolate, spreading, towards base joined loosely into 5-7 angles along stem, above conical, tapering into slender acuminate soft tooth. Inflorescence of 1-5 flowers developing successively from stout knobby peduncle up to 10 mm long with many slender acuminate bracts 3-5 mm long; pedice/ 10-16 mm long, 1.5 mm thick, spreading and holding flower facing horizontally; sepals 5-9 mm long, 1 mm broad at base, slender, acuminate, usually much exceeding sinuses of corolla lobes. Corolla 35-45 mm diam., rotate; outside smooth, cream to pinkish on tube, with 1 heavy (2 lighter) raised longitudinal veins running from tip of lobe to base of tube; inside cream or yellow on lobes becoming suffused with pink outside mouth of tube then maroon in tube changing to white towards base, with very low papillae each tipped with a fine spike-like usually dark maroon bristle on lobes and inwards as far as mouth of tube; tube 2-3 mm long, 8-10 mm broad at mouth, shallowly bowl-shaped, obscurely pentagonal; lobes 12-16 mm long, ± 5 mm broad at base, horizontally spreading, convex above, narrowly lanceolate, attenuate. Corona 2.5 mm tall, 3-4 mm broad, ± without basal stipe; outer lobes spreading, laterally fused into obscurely pentagonal to almost circular disc (rarely distinctly 5-lobed), cream; inner lobes ± 0.3 mm long, cream suffused with maroon, adpressed to backs of anthers and shorter than them, with very enlarged spreading to ascending obtuse dorsal gibbosity 0.5-0.7 mm long at base, tapering to narrowly obtuse bristly apex.

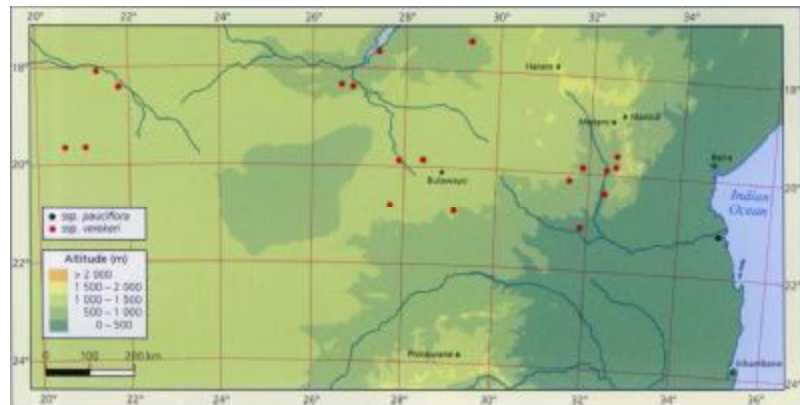


Fig. 5.4. Distribution of *Huernia verekeri* in southern Africa.

This species is widespread across the northernmost part of southern Africa from the Chela Mountains in southern Angola to the coastal plains of central Moçambique, south of Beira.

Leach (1969a; 1974a) established three varieties of *H. verekeri*: var. *angolensis* in southern Angola, var. *verekeri* that is widespread across tropical southern Africa, and var. *pauciflora* from the coastal parts of central Moçambique. Both var. *angolensis* and var. *pauciflora* have somewhat creeping stems (in var. *angolensis* with very rounded angles with reduced tubercles as well) and both are geographically far removed from var. *verekeri*. They are recognised here at subspecific rank.

1a. *Huernia verekeri* subsp. *verekeri*

Huernia verekeri var. *stevensonii* A.C. White & B. Sloane, Stap., ed 2, 3:145 (1937).

Type: Zimbabwe, Nyamandhlovu distr., near Sawmills, Stevenson (missing).

Stems 8-12 mm thick, decumbent; tubercles 8-15 mm long, laterally flattened towards bases, joined into (5-) 6 (-7) angles along stem. Inflorescences of 1-5 flowers developing in rapid succession. Corona: outer lobes forming obscurely pentagonal to almost circular disc (rarely distinctly 5-lobed); inner lobes with spreading to ascending obtuse dorsal gibbosity.

Distribution and habitat

Subsp. *verekeri* is very widespread indeed and occurs in Botswana, Malawi, Moçambique, Namibia, Zambia and Zimbabwe. In Namibia it occurs only in the north-eastern region between Tsumkwe and Andara (the locality given by Leach (1988) for the Kaokoveld is an error, according to W. Giess [pers. comm. 1993] and it is found too in the adjoining part of Botswana from Nokaneng northwards to

Key to the subspecies of <i>H. verekeri</i> (for southern Africa only)	
Stems decumbent, mainly 6-angled with tubercles 8-15 mm long	1a. subsp. <i>verekeri</i>
Stems prostrate, 9-angled with tubercles 3-6 mm long	1b. subsp. <i>pauciflora</i>

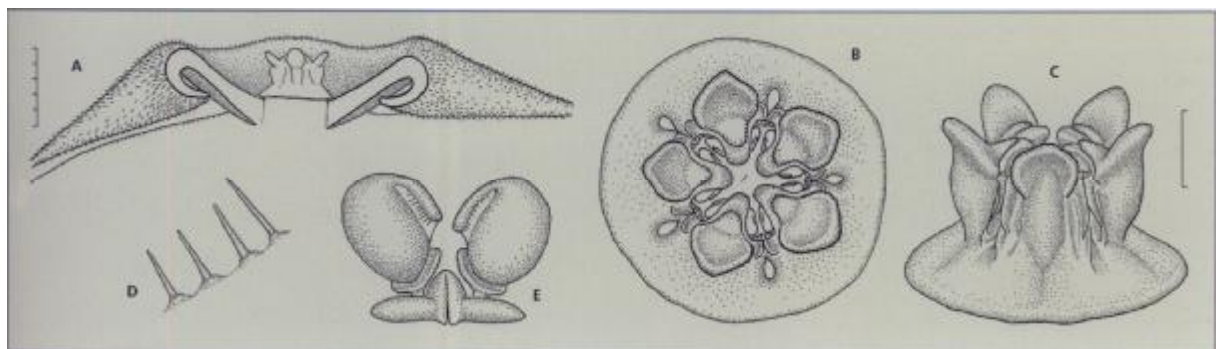


Fig. 5.5. *Huernia verekeri* subsp. *verekeri*. A, side view of dissected flower. B, face view of gynostegium. C, side view of gynostegium. D, papillae inside corolla at base of lobes. E, pollinarium. Scale bars: A, 5 mm; B, C, 1 mm (at C); D, 0.5 mm (at C); E, 0.25 mm (at C). Drawn from PVB 4125, east of Tsumkwe, Namibia.

HUERNIA VEREKERI

Shakawe on the western bank of the Okavango River. In these areas it usually grows in grey to white sand at the foot of trees and is quite often associated with *Acacia nigrescens*.

In Zimbabwe subsp. *verekeri* is more widespread. Here it grows in the west between Hwange and Gokwe, in the north along the Zambezi River (where it has also been recorded in the neighbouring parts of Zambia), and in the east in the low-lying valley of the Sabi River. There are records as well from the middle reaches of the Shire River in Malawi in the Mpatamanga Gorge and in the Tete Province of Moçambique. In all these areas it grows in stony places in valleys under trees or shrubs.

Diagnostic features and relationships

In subsp. *verekeri* the stems are erect to spreading and may form quite large and untidy clumps. The tubercles on the stems are loosely arranged into 5-7 angles, each usually attenuating into a slender, soft tooth.

In all subspecies of *H. verekeri* the flower is very similar. It consists of slender, attenuated lobes and a shallow, bowl-shaped tube in the middle. The lobes are convex above for most of their length from somewhat reflexed margins. They are slightly reflexed around the mouth of the tube but the tissue is not thickened there, so there is no obvious annular ridge. Inside, the lobes and the small united part beyond the mouth of the tube are cream and there is an abrupt change to maroon just within the mouth of the tube. This colour gradually fades to white in the base around the corona. The cream parts are covered with fine, dark bristles, each of which arises from a very low papilla (see fig. 28 E for a close-up of these structures). These bristles and papillae vanish suddenly just within the mouth of the tube.

In the base of the tube there is a relatively small gynostegium. This has a very short, disc-like outer corona which descends to and touches the base of the tube but is not fused to it underneath. There are also very short inner corona lobes, usually not even as long as the anthers. Each of them has a quite tall, slightly spreading, dorsal gibbosity which is longer than the lobe itself.

There are many features of the flower here which are shared with *Duvalia*. In the morphological analysis, *H. verekeri* was found to be sister to all the other species of *Huernia*. The corolla lobes have somewhat reflexed margins, so they are convex above (rather than concave above), which is more typical of *Duvalia*. Furthermore, the shape of the papillae inside the corolla is unusual for *Huernia*. The lack of a tubercle beneath the guide-rail on the outer coronal disc and the relatively large dorsal protrusions on the inner lobes makes the gynostegium similar to that found

in *Duvalia*. Moreover, the pollinia are unusually short and broad, with particularly long wings on the corpuscle.

History

White & Sloane (1937:849) told of the discovery of this species, which was named after Louis Stanhope Amos Vereker (? 71874-12 March 1948). Vereker farmed for a time at Rumani near Harare and made several watercolour paintings of local orchids. *Huernia verekeri* was first noticed by Vereker's assistant D.H.

Townley who, during an expedition to the lower Sabi Valley, brought back a withered specimen after being out looking for birds. Vereker threw the plant out, believing it to be the ubiquitous *H. hislopilii*. However, something must have suggested to him that he might have made a mistake and, on searching the locality later when passing it again on their trip, he found a plant in flower which confirmed his suspicion that it was not *H. hislopilii*. Plants collected then were cultivated at H. Basil Christian's garden at Ewanrigg and they were later described by Ms. Sydney Stent.



Fig. 5.6. *H. verekeri* subsp. *verekeri*, PVB 4125, east of Tsumkwe, Namibia.



Fig. 5.7. *H. verekeri* subsp. *verekeri*, PVB 6489, south of Shakawe, Botswana.

1b. *Huernia verekeri* subsp. *pauciflora*

Huernia verekeri subsp. *pauciflora* (L.C. Leach)
Bruyns, stat. nov.

Huernia verekeri var. *pauciflora* L.C. Leach, *Bothalia*
10: 49 (1969).

Type: Moçambique, near Save R. mouth, south of
Mambone, Leach & Bayliss 11889 (SRGH holo.,
K, LISC, PRE, iso.).

Stems 6-10 mm thick, prostrate; tubercles 3-6 mm long, not laterally flattened, joined into 5 obtuse angles along stem. Inflorescence of 1-3 flowers developing in gradual succession. Corona: outer lobes forming obscurely pentagonal disc; inner lobes with spreading and obtuse dorsal gibbosity.

Distribution and habitat

Subsp. *pauciflora* is recorded with certainty only from south of Mambone near the mouth of the Save (Sabi) River (Leach 1988) and has recently been recollected in that area.

It occurs here at 2-5 m above sea level in flat plains covered with short grass and with isolated, dense, forest-like thickets dominated by trees of *Androstachys johnsonii*, the Lebombo ironwood, which is locally known as *M'Crusse*. Subsp. *pauciflora* flourishes on the floor of these small 'forests', where it grows in deep shade in leaf-litter. These remarkable forest-clumps support a wealth of other succulents, including *Sansevieria*, *Ceropegia ampliata*, *C. stapeliiformis*, *Aloe cryptopoda*, several species of *Euphorbia*, *Pterodiscus*, *Adenium*, *Raphionacme* and *Orbea umbracula*.

Diagnostic features and relationships

Subs. *pauciflora* forms diffuse and fairly small clumps, which may reach 20 cm in diameter, with creeping, sparingly branched stems which root all along their length. The tubercles are shorter and more widely spaced than in subsp. *verekeri* and form usually five, somewhat rounded angles along the stems, with each



Fig. 5.8. *H. verekeri* subsp. *pauciflora*, PVB 7681, south of Mambone, Inhambane Province, Moçambique.

tubercle tapering into a fairly short tooth.

In this subspecies the flowers are produced in smaller numbers and they open in gradual succession on each inflorescence. The corolla in both subspecies is very similar. Slight differences have been noted in the respective coronas of the two subspecies. In subsp. *pauciflora* the outer coronal disc is smaller than the breadth of the top of the corona and the dorsal gibbosity on the inner lobes spread out horizontally.

History

Subsp. *pauciflora* was discovered by L.C. Leach and Roy D.A. Bayliss on 9 October 1963 (Leach 1970a: 45) south of Mambone in central Moçambique. It was recorded again in this

area for the first time in December 1998. Leach (1988) cited another collection (*Huntington Bot Garden* 21952) which was reputed to have come from Gorongosa in Moçambique. However, enquiries at Huntington (J. Trager, pers comm. 2002), revealed that this was a collection made by Bayliss and it is therefore very likely to have been part of the type, as Bayliss is not known to have collected in Gorongosa. Consequently this locality is left off the map.

[*Huernia verekeri* subsp. *angolensis* (L.C. Leach)

Bruyns, stat. nov.

Huernia verekeri var. *angolensis* L.C. Leach, *J. S. African Bot.* 40: 19 (1974).

Type: Angola, Huila distr., Leach & Cannell 14650 (LISC, holo.; BM, LUAI, PRE, SRGH, iso.)]

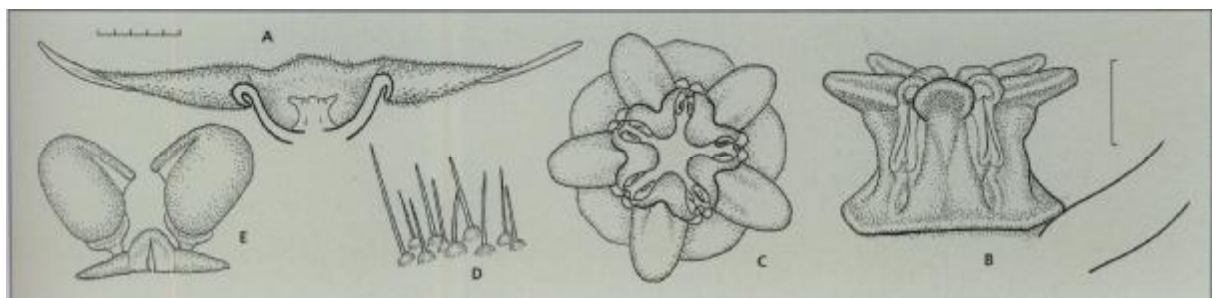


Fig. 5.9. *Huernia verekeri* subsp. *pauciflora*. A, side view of dissected flower. B, side view of gynostegium. C, face view of gynostegium. D, papillae inside corolla at base of lobes. E, pollinarium. Scale bars: A, 5 mm; B, C, 1 mm (at B); D, 0.5 mm (at B); E, 0.25 mm (at B). Drawn from PVB 7681, south of Mambone, Inhambane Province, Moçambique.

HUERNIA PROCUMBENS

2. *Huernia procumbens*

Huernia procumbens (R.A.Dyer) L.C. Leach,

Bothalia 10: 54 (1969).

Duvalia procumbens R.A.Dyer, *Fl. Pl. Africa* 31: t.

1218 (1956).

Type: South Africa, Transvaal, Pafuri, Van der Schijff 3618 (PRE).

Small succulent forming prostrate mats up to 500 mm diam. *Stems* 60-500 mm long, 7-12 mm thick, prostrate (if erect then soon arching back to soil) sometimes becoming pendent from rocks, green to purplish; *tubercles* very obtuse and hardly rising out of stem, joined into 5 obtuse angles along stem, each bearing spreading lanceolate leaf-rudiment 2-3 mm long at apex. *Inflorescence* of 1-5 flowers developing in gradual succession from peduncle (up to 15 mm long), with several slender bracts 2-4 mm long; *pedicel* 10-15 mm long, 1.5 mm thick, spreading with erect apex holding flower facing upwards; *sepals* 8-11 mm long, 1.5 mm broad at base, narrowly attenuate. *Corolla* 30-55 mm diam. when rotate to with lobes fully reflexed (then 8-15 mm diam.); outside smooth, pink mottled on cream to uniformly pale pink with 1 raised longitudinal vein running down centre of each lobe; inside cream on lobes becoming pink to maroon near and on annulus, with very fine red spike-like papillae on lobes (where longest) and often on annulus; *tube* $\pm$ 1 mm deep, bowl-shaped, with corolla strongly reflexed below bases of lobes around mouth to form apparent annulus; *lobes* 13-24 mm long, 4-5 mm broad at base, spreading to reflexed, narrowly lanceolate, acuminate, convex towards base and concave towards apex, with red margins. *Corona* 2.5-3.0 mm tall, 3.5 mm broad, pink to pale maroon, very slightly raised on minute stipe; *outer lobes* 0.5 mm long, broadly obtuse, spreading and filling up base of tube; *inner lobes* < 0.5 mm long, adpressed

to backs of anthers and shorter than them, dorsiventrally flattened, obtuse, with large obtuse ascending to erect dorsal projection $\pm$ 1.5 mm long flattened above and with rear extending down to level of outer lobes.

Distribution and habitat

Huernia procumbens is a very localised species that is found in a small area around the north-easternmost corner of South Africa and in the adjacent part of Zimbabwe. In South Africa it is found west of Pafuri on steep banks of the Luvuvhu River and further westwards to around the village of Masisi.

Plants of *H. procumbens* grow on the southern aspect of low hills and river valleys under 'forests' of the Lebombo ironwood *Androstachys johnsonii*. They usually grow on rock outcrops or on rock-ledges, in shallow soil supplemented by accumulations of leaf-litter.

Diagnostic features and relationships

As the name suggests, in *H. procumbens* the stems are prostrate and creep for a length of up to 500 mm, rooting and branching along their entire length so that they form often quite diffuse mats. As is frequently the case with species with a prostrate habit (though not for *H. verekeri* subsp. *pauciflora*), the stems have very obscure tubercles and are nearly cylindrical. Branches are very weakly attached and fall off on being moved even slightly but such detached pieces root again and establish separate plants very readily.

Flowers of *H. procumbens* are quite unusual, with long, slender lobes that may be



Fig. 5.10. Distribution of *Huernia procumbens*.

strongly reflexed. The lobes radiate from somewhat below the small and sharply raised, apparent annulus in the centre. Inside, there is a fine dark margin along the otherwise cream lobes and the centre of the flower also contrasts by being pink to maroon. The inside of the corolla is not at all shiny. If the centre of the flower is sectioned, it will be seen that the 'annulus' is not actually any thicker than the rest of the corolla and that it is formed by the abrupt reflection of the corolla a little below the bases of the lobes and not by the usual thickening of the corolla (as one finds in species of *Duvalia*). This is therefore a particularly good example of a false annulus.

The corona is a similar colour to the centre

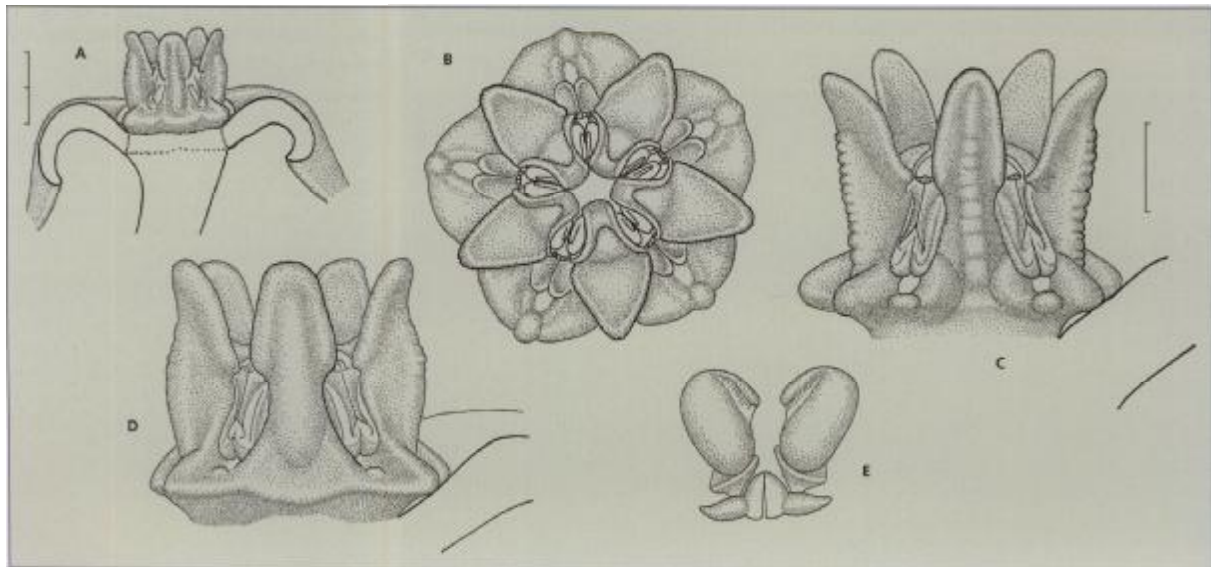


Fig. 5.11. *Huernia procumbens*. A, side view of centre of dissected flower. B, face view of gynostegium. C, D, side view of gynostegium. E, pollinarium. Scale bars: A, 2 mm; B-D, 1 mm (at C); E, 0.25 mm (at A). Drawn from A, D, PVB 6589, near Tshikondeni; B, C, E, PVB 2075, near Masisi.



Fig. 5.12. *H. procumbens*, PVB 2075, near Masisi.



Fig. 5.13. *H. procumbens*, PVB 6589, near Tshikondeni.



Fig. 5.14. *H. procumbens*, PVB 6589, near Tshikondeni, flowering in habitat among leaf-litter and other debris on ledges of low, rocky ridge, January 1996.

of the corolla and, by the manner in which the corolla lobes fold backwards, it is pushed somewhat forwards beyond the flower. This phenomenon is unusual for *Huernia* but is also known in *Orbea umbracula*. There are small outer lobes that form a nearly disc-like structure around the base of the gynostegium. Beneath this disc the gynostegium tapers off towards its base to form a slight stipe. The inner lobes are very small on the backs of the anthers and the whole gynostegium is, in fact, dominated by their relatively massive, nearly erect, dorsal projections. These projections are nearly the same length as the height of the gynostegium below them and they are 3-5 times as long as the lobes themselves.

Huernia procumbens is, even for *Huernia*, where there is such a high level of diversity, a most unusual species. It has its closest relative in *H. tanganyikensis* which occurs around the foot of Mt Kilimanjaro in Kenya and Tanzania. Perhaps most important, though, is the fact that it shares several characters with *Duvalia*. In particular, the lack of a tubercle at the base of the guide-rails, the very prominent dorsal projection on the inner corona lobes and a very small stipe supporting the gynostegium are all features similar to those seen in *Duvalia*.

Another aspect of this species, which

has not been adequately noted before, is the remarkable similarity that it has in many features to *H. verekeri*. The colour scheme of the flowers is the same; the surface of the flower is covered with similar papillae, especially on the lobes; the lobes are unusually long and narrow in both species; both lack the tubercle at the base of each guide-rail; and they have similar, very prominent dorsal projections on the inner lobes. As noted by Leach (1974a), the corolla lobes are slightly concave on the upper surface towards their apices and this is more typical of *Huernia* and is unknown in *Duvalia*.

History

Huernia procumbens was first collected by L.E. Codd in March 1949 and a bit later by H.P. van der Schijff in 1954. Both of these collections were made during inventories of the flora of the Kruger National Park in South Africa. Van der Schijff's material flowered in cultivation in Pretoria in February 1955 and from this the species was described. R.A. Dyer described it as *Duvalia procumbens*, to conform with *D. tanganyikensis*, but it was shown by Leach (1969a) that it fitted better into *Huernia*.

3. *Huernia urceolata*

Huernia urceolata L.C. Leach, *Fl. PL Africa* 39: t. 1550 (1969).

Type: Angola, Mocamedes distr., Leach & Cannell 14025 (PRE, holo.; K, LISC, iso.).

Small succulent forming clumps 100-500 mm diam. Stems 20-150 mm long, 15-25 mm thick (excluding teeth), erect, grey-green mottled with purple; tubercles 10-15 mm long, narrowly deltoid, spreading, laterally flattened, joined towards base loosely into 5 often spirally twisted angles along stems, acuminate. Inflorescence of 1-5 flowers developing in gradual succession on short peduncle; pedicel 7-10 mm long, 1.5 mm thick, ascending then spreading to hold flower facing horizontally or nodding; sepals 4-10 mm long, 1.0-1.5 mm broad at base, narrowly ovate, attenuate. Corolla 9-12 mm long, 10-14 mm broad, globose-urceolate; outside smooth, purplish to pale red, with 1 heavy (and sometimes 2 fainter) raised longitudinal veins running from apex of lobe and fading on corolla tube; inside smooth, deep velvety purple-red on lobes to middle of tube with broad ring of white below middle of tube changing again to deep maroon around corona; tube 8-12 mm long, 5-8 mm broad at mouth, constricted towards mouth, not pentagonal; lobes 4-5 mm long, 4-7 mm broad at base abruptly narrowing to ± 2 mm, spreading and partly recurved, narrowly acute. Corona ± 3 mm tall, 5 mm broad, deep red with blackish rim on outer lobes, slightly raised above base of corolla on very short stipe; outer lobes < 1 mm long, fused into obtusely pentagonal disc around gynostegium, descending so that edges of disc touch base of corolla tube; inner lobes < 1 mm long, adpressed to backs of anthers but not exceeding them, $\pm$ ovate, very fleshy and swollen dorsally behind base.

Distribution and habitat

Huernia urceolata occurs in the north-western corner of Namibia, primarily in the northern Kaokoveld. Here it is found from north of Opuwa to the Otjijhipa, which are situated somewhat west of the Baynes Mountains. It is also recorded sporadically eastwards along the Kunene River to near Ruacana Falls. In this area

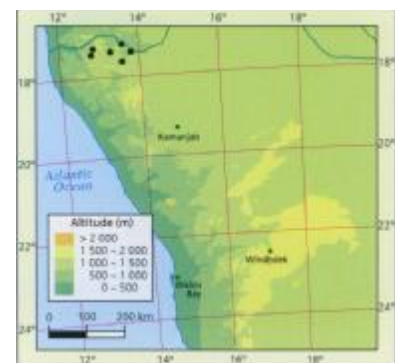


Fig. 5.15. Distribution of *Huernia urceolata* in southern Africa.

HUERNIA URCEOLATA

it is mostly found at altitudes of over 1 000 m except for a few spots along the Kunene River, where it occurs as low as 700 m. In Angola it is known in the Benguela and Namibe (Mocamedes) districts.

Plants may be locally quite plentiful but are usually few and far between and have been seen mainly between scattered trees of *Colophospermum mopane* growing among rocks and small bushes, often with *Huernia oculata* and *Hoodia parviflora*. In the Otjihipa and Okakora, specimens were seen on several occasions on steep slopes with *Myrothamnus flabellifolius*, *H. parviflora*, the small fern *Actiniopteris* and *Euphorbia eduardoi* so it is not very particular about the habitat in which it grows.

Diagnostic features and relationships

Plants of *H. urceolata* may become quite large and they usually have stout, robust stems up to 150 mm tall and 25 mm thick. The tubercles taper into long, spreading, slender and soft teeth and are slightly flattened above. They are rather untidily and loosely arranged into five often somewhat spiralling angles.

The remarkable flowers of this species are unmistakable. They arise in small groups near the bases of the stems and are usually slightly nodding. The corolla is not particularly large (not more than 15 mm in diameter and usually slightly shorter than broad) but it has an extraordinary globose-urceolate shape. This shape is clear already in the bud where the lobes form a small protrusion near the apex and the tube occupies most of the corolla. In the bud another unusual feature is the manner in which folds at the bases of the lobes project



Fig. 5.16. *H. urceolata*, PVB 4085, Okonguati, Namibia, in habitat, January 1990, with stems nearly 20 cm tall.

upwards (relative to the rest of the flower) as five small, slender prongs. When the flower opens they spread out so as to assume a more normal attitude but are relatively large in the mature flower and may reach nearly half the size of the lobes themselves. The lobes are slender and relatively small, spreading from the mouth of the tube.

The flowers are pale red outside but inside are unexpectedly pretty with a deep velvety red on the lobes that changes abruptly to a band of white in the middle of the tube and changes again to maroon lower down around the corona. They smell quite strongly of formic acid.

In *H. urceolata* the gynostegium is also unusual. The whole structure is more than usually short and it is nearly twice as broad as tall. The outer lobes form a slightly pentagonal disc which descends to the base of the corolla tube but is not fused to it. The inner lobes are fairly short but are exceptionally broad and expand towards their much inflated base. There is no trace of the dorsal gibbosity which is found in all species of *Huernia* except this one and *H. concinna*.

The appearance of the plant in *H. urceolata* suggests an outsize specimen of *H. oculata*, with which it has been found to occur in many localities, and the colouring inside the

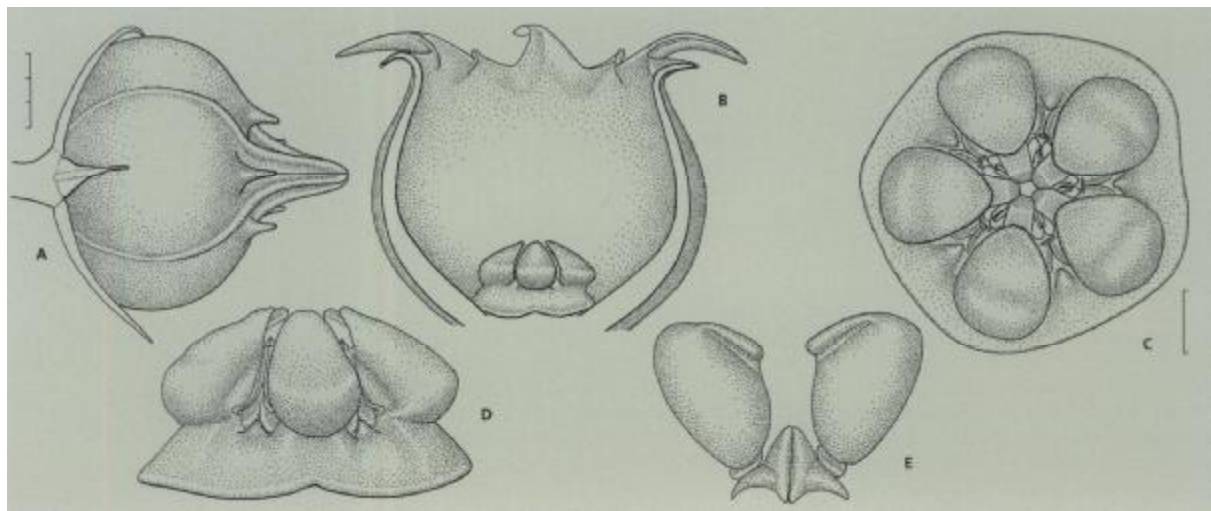


Fig. 5.17. *Huernia urceolata*. A, bud. B, side view of dissected flower. C, face view of gynostegium. D, side view of gynostegium. E, pollinarium. Scale bars: A, B, 3 mm (at A). C, D, 1 mm (at C); E, 0.25 mm (at C). Drawn from PVB 4085, Okonguati, Namibia.

corolla also hints that these two species may be related. However, the gynostegium is very different, and in fact is unlike that of any other southern African species, being more similar to that of *H. concinna* of Somalia. Nevertheless, other morphological characters do not support a close relationship between these two.

History

Leach (1969b) found that this species was first collected in January 1956 by the Portuguese botanist Eduardo J. Mendes at Vila Arriaga near Namibe and Leach himself recollected it in much the same area in 1967. Around the same time (that is, in 1968) it was collected at Otjipemba in the Kaokoveld of Namibia and, at the time of his revision (Leach 1988), this was the only record from Namibia. Recent collecting has shown it to be quite widespread in the Kaokoveld but it does not seem to occur any further south.



Fig. 5.18. *H. urceolata*, PVB 4085, Okonguati, Namibia.



Fig. 5.19. *H. urceolata*, PVB 5604, east of Epupa Falls, Namibia. The white band in the tube may be seen here.

4. *Huernia oculata*

Huernia oculata Hook. f., Bot. Mag. 108: t. 6658 (1882).

Type: Namibia, Damaraland, Een (K).

Huernia rogersii R.A.Dyer, Rec. Albany Mus. 3: 468 (1927).

Type: Namibia, Omaruru, FA, Rogers (missing).

Dwarf succulent forming clump to 300 mm diam. Stems 20-150 mm long, 8-15 mm thick (excluding teeth), erect, purplish green often flecked with maroon; *tubercles* 7-12 mm long, spreading, deltoid, laterally flattened and joined into 5 angles along stem, tapering into slender caducous tooth. *Inflorescence* with many flowers developing in rapid succession from short stout peduncle, with narrowly attenuate bracts 4-8 mm long at base; *pedicel* 4-6 mm long, 1 mm thick, ascending to spreading and usually with decurved apex holding flower facing horizontally or slightly downwards; *sepals* 8-15 mm long, < 1 mm broad at base, narrowly ovate-attenuate, papillate on exterior. *Corolla* 5-7 mm long, 18-24 mm diam., shallowly bowl-shaped; outside greenish becoming cream flecked with maroon towards base, covered with low conical papillae, with one heavy and 3-4 lighter raised longitudinal veins running down from lobes; inside white (sometimes pinkish and with fine maroon spots towards base), abruptly changing at middle of tube to deep maroon-black (rarely green) above, covered with minute columnar papillae usually tipped with small bristle, papillae usually same colour as background though often pale maroon around corona; tube $\pm$ 4-5 mm deep, bowl-shaped, widening from base to mouth; *lobes* 4 mm long, 7-9 mm broad at base, broadly deltate, somewhat acuminate, spreading. *Corona* 3.5 mm tall, 3.5-4.5 mm broad, buff to white speckled with maroon, slightly raised above base of corolla on very short stipe; *outer lobes* $\pm$ 0.5 mm long, descending to surface of corolla so that apex adpressed to it, $\pm$ semicircular-emarginate in outline; *inner lobes* $\pm$ 2 mm long, adpressed to backs of anthers, dorsiventrally flattened, with transverse dorsal gibbosity $\pm$ 1.25 mm wide at base, beyond anthers rising up slightly to small bristly obtuse pale apex.

Distribution and habitat

Huernia oculata is certainly the most common species of *Huernia* in the tropical parts of Namibia. It is fairly plentiful from Karibib and Windhoek northwards to the Kaokoveld and then eastwards to Tsumeb and Grootfontein. It mainly occurs east of the driest part of the Namib, though it is also quite plentiful between Rocky Point and Sarusas along the Skeleton Coast and within 30 km of the sea. On the eastern side of Namibia it is mainly confined by deep Kalahari sands, in which it rarely occurs, and by the higher rainfall of Ovamboland and the Caprivi. There are two records from south-western Angola in the vicinity of Namibe (Leach 1988).

Plants grow occasionally in sand under bushes but are most frequently found on stony patches of calcrete amongst acacias and other

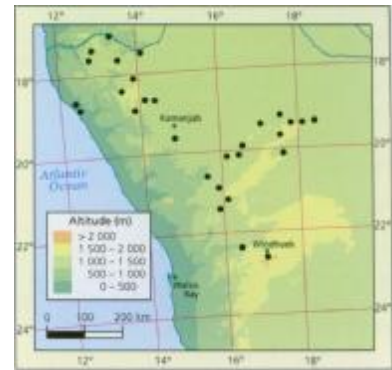


Fig. 5.20. Distribution of *Huernia oculata* in southern Africa.

spiny shrubs, often with other stapeliads such as *Orbea lugardii*, *O. lutea*, *Stapelia schinzii* and *Tavaresia barklyi*. Along the Skeleton Coast they occur in crevices in granite outcrops.

Diagnostic features and relationships

This is one of the most distinctive species of *Huernia*. The stems usually form a fairly dense clump. In plants in the Namib they are very short (20-40 mm long) but further east they may be considerably longer and quite often exceed 80 mm in length. The tubercles are flattened and joined into thin, continuous and sometimes slightly spiralling wing-like angles along the stem. Each of them tapers into a slender, soft tooth which is slightly flattened on the upper surface.

In *H. oculata* the flowers may be produced in quite large numbers that open in close succession on peduncles around the base of the plant. The relatively short pedicel often holds the flower in a nodding attitude and has remarkably long and slender sepals at its apex which usually exceed the length of the corolla tube. The flower is fairly small (usually about 20 mm across) and consists mainly of a bowl-shaped tube with the small, broad lobes hardly spreading at all around its mouth. The outside of the flower is often dark towards the base and is somewhat rough with papillae. On the inside there is a remarkable combination of colours. The lobes and about half of the tube are a very dark maroon that could easily be mistaken for black. This dark colour stops abruptly in about the middle of the tube and changes to white. Lower down towards the base this white area is finely speckled with maroon or may become pinkish speckled with maroon. There are small papillae over much of the interior of the corolla (see fig. 28 A).

The nearly cylindrical gynostegium in the centre of the flower is off-yellow to white and finely speckled with maroon. It consists of very

HUERNIA OCULATA

short outer corona lobes which descend steeply to the base of the corolla without spreading there at all. The small, finely papillate inner lobes meet in the centre and exceed the anthers but do not rise up in a column.

History

Huernia oculata was discovered by the Danish trader and collector Ture Johan Gustaf Een between 1878 and 1880 in Damaraland in Namibia. He brought plants to Kew, where they flowered in June 1880 and were described a little over two years later by J.D. Hooker.



Fig. 5.21. *H. oculata*, PVB 5495, north of Grootfontein, Namibia.



Fig. 5.22. *H. oculata*, PVB 5528, east of Waterberg, Namibia.



Fig. 5.23. *H. oculata*, PVB 5549, north of Sesfontein, Namibia, in habitat, February 1993. (photo: G.D. Tribe)

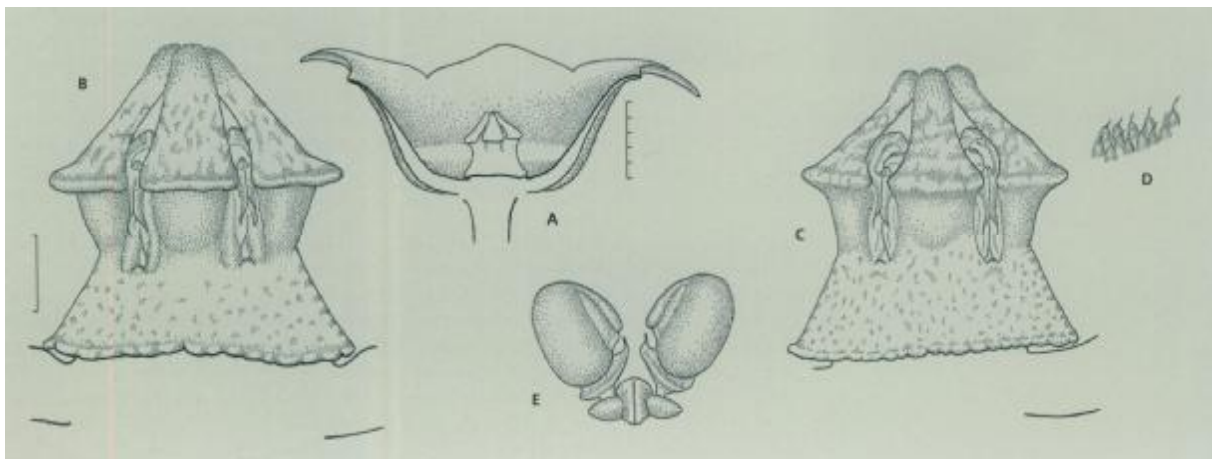


Fig. 5.24. *Huernia oculata*. A, side view of dissected flower. B, C, side view of gynostegium. D, papillae inside corolla in mouth of tube. E, pollinarium. Scale bars: A, 5 mm; B, C, 1 mm (at B); D, 0.5 mm (at B); E, 0.25 mm (at B). Drawn from A, B, Downs, ± 30 miles north-east of Namibe, Angola; C-E, PVB 8034, west of Etengwa, Namibia.

5. *Huernia leachii*

Huernia leachii Lavranos, J. S. African Bot 25: 311 (1959).

Type: Moçambique, Chimoio (Vila Pery), Leach 5641 (PRE).

Small succulent forming spreading mats covering up to 2 sq. m diam. Stems 30-300 (-500) mm long, 3-8 mm thick, procumbent, sometimes ascending slightly towards apex, pale green to reddish; *tubercles* 3-4 mm long, very obscure, low and rounded and joined into 4 (-5) obtuse and obscure angles along stem, abruptly narrowed into ascending to spreading lanceolate acute leaf-rudiment $\pm$ 2 mm long. *Inflorescence* of 1-6 flowers developing in gradual succession on peduncle up to 10 mm long with few filiform bracts 2-4 mm long; *pedicel* 5-40 mm long, 1 mm thick, ascending then descending towards apex to hold flower facing partly downwards ($\pm$ nodding); *sepals* 5-7 mm long, 1 mm broad at base, slender and attenuate. *Corolla* 10-17 mm long, 20-25 mm diam., bowl-shaped; outside papillate, pale pinkish green, with 2-5 longitudinal raised veins running down each lobe onto tube; inside cream with broken (on lobes where sometimes only very faint) to continuous (in tube) narrow concentric maroon stripes and solid maroon patch in base of tube, with cylindrical obtuse papillae longest (< 1 mm) in mouth of tube; *tube* $\pm$ 6 mm long, 12 mm broad at mouth, bowl-shaped, slightly pentagonal, without thickening around mouth; *lobes* 6 mm long, 7 mm broad at base, ascending to spreading, deltate, acute. *Corona* $\pm$ 3.5 mm tall, 3.0 mm broad, dark maroon except on inner lobes, without basal stipe; *outer lobes* $\pm$ 0.5 mm long, dark maroon, margins rounded or emarginate, spreading on base of tube; *inner lobes* $\pm$ 1.5 mm long, yellow with dark maroon margins, adpressed to backs of anthers near bases, ascending to meet in centre, linear from slightly swollen dorsal gibbosity to obtuse bristly apex.

Distribution and habitat

Huernia leachii is known from several patches around the type locality near Mt Zembe, which lies to the south of Chimoio in central Moçambique. It also occurs near Catandica (formerly Vila Gouveia), about 125 km north of the type locality. It is possibly also known from a single gathering in Malawi, which was made on the south-western shores of Lake Malawi near Monkey Bay, about 500 km to the north of Catandica.

Around Mt Zembe *H. leachii* occurs on gently sloping, granite 'whale-backs', closely intermingling with the coarse, tough, dense, perennial, tussock-forming sedge *Coleochloa*, *Xerophyta*, *Euphorbia granitcola*, *Aloe cameronii* and *A. chabaudii* *Sarcostemma viminale* and sometimes with *H. hislopii*. Near Catandica plants were found with the same species, *Euphorbia griseola* and *Myrothamnus flabel-lifolius*. They are locally extremely common, growing in shallow accumulations of weathered granitic grit and leaf-litter.

Diagnostic features and relationships

Huernia leachii is a very unusual species, with slender, almost terete stems which taper into a very fine tip when actively growing. In habitat they form entangled, often fairly sparse mats which spread over an area of up to 2 sq m. The stems are mostly prostrate and creeping, rooting as they go along. New growth is often extremely vigorous, with the slender stems giving the impression of 'shooting' out in all directions. These new stems bear quite conspicuous, slender, sharp-tipped but soft leaf-rudiments at intervals varying up to 20 mm and the rudiments in a pair are not always strictly opposite. The tubercles on which they

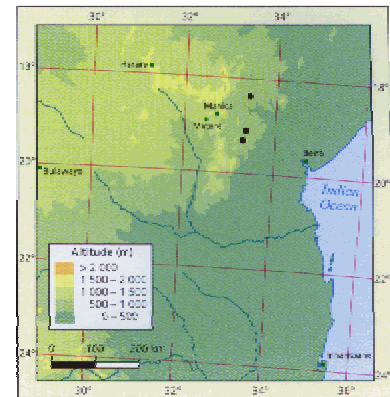


Fig. 5.25. Distribution of *Huernia leachii* in southern Africa.

are borne are hardly visible at all. Young stems are shiny green to reddish.

Flowering in *H. leachii* is somewhat sparse and the flowers are unusual, both in their shape and because of the fairly strong odour of excrement that they emit. The corolla is shallowly bowl-shaped with the lobes continuing from the tube and hardly spreading at all at its mouth. Outside it is somewhat scabrid with small, obtuse papillae. Inside it is prettily marked with narrow, concentric, maroon lines on a cream background and these markings are most conspicuous in the tube. There is a dark maroon patch around the corona.

The corona consists of relatively short, rounded, dark maroon outer lobes pressed to the base of the tube and short inner lobes rising slightly above the anthers to gather in the centre. The inner lobes are yellow with maroon along their margins.

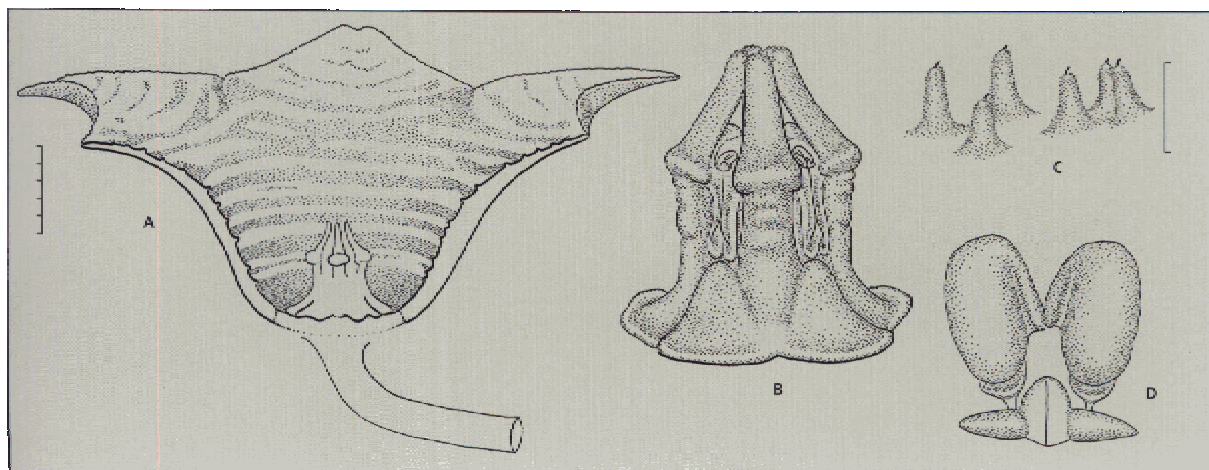


Fig. 5.26. *Huernia leachii*. A, side view of dissected flower. B, side view of gynostegium. C, papillae inside corolla in mouth of tube. D, pollinarium. Scale bars: A, 5 mm; B, 1 mm (at C); C, 0.5 mm; D, 0.25 mm (at C). Drawn from A, C, D, PVB 7404, west of Mt Zembe, Manhiça Province, Moçambique; B, PVB 7398, north of Mt Zembe, Manhiça Province, Moçambique.

HUERNIA LEACHII

South of Chimoio *H. leachii* grows in profusion with *H. hislopilii*, and hybrids between them are common. In the hybrids the stems are decumbent and 5-8 mm thick, with more prominent tubercles than in *H. leachii*. Flowers are also intermediate, with a deeper tube than in *H. leachii*, longer lobes and shorter markings on the lobes and mouth of the tube. Lower in the tube there are concentric rings of maroon as in both species. Papillae in the tube are more prominent than in *H. leachii* but not nearly as large as in *H. hislopilii* and the corona too, is intermediate, with longer inner lobes than in *H. leachii*.

History

Huernia leachii was discovered near Mt. Zembe, south of Chimoio (formerly Vila Pery), in Moçambique in 1956 by L.C. Leach. The material sent to Leach from Malawi by Theo Campbell-Barker was supposed to have been discovered near Monkey Bay on Lake Malawi in 1975 by a Mr. Brussow.



Fig. 5.27. *H. leachii*, PVB 7404, west of Mt Zembe, Manhica Province, Moçambique.



Fig. 5.28. *H. leachii*, PVB 8746, east of Catandica, Manhica Province, Moçambique.



Fig. 5.29. *H. leachii*, PVB 7398, north of Mt Zembe, Manhica Province, Moçambique.



Fig. 5.30. *H. leachii*, PVB 7398, north of Mt Zembe, Manhica Province, Moçambique, on a low, granite dome at the foot of a plant of *Euphorbia graniticola*, December 1997.

6. *Huernia pendula*

Huernia pendula E.A. Bruce, *Fl. Pl. Africa* 28: t. 1108 (1953).

Type: South Africa, Eastern Cape, Kei River near Ngancule, E.A. Phillips 1 (PRE).

Small succulent forming mats 150-500 mm diam. on ledges on cliffs with some pendent stems. Stems 150-500 mm (~1.5 m) long, 3-8 mm thick, trailing to pendent, if initially erect then soon arching back to ground and rooting, grey-green to green to purplish; tubercles very obscure so that stem $\pm$ cylindrical. Inflorescence of 1-5 flowers developing in gradual succession from gradually elongating peduncle (up to 20 mm long) with few deltoid to lanceolate bracts (< 2 mm long), arising mainly towards base of stem but also along stem towards and at apex; pedicel 7-10 mm long, $\pm$ 1.5 mm thick, descending and holding flower nodding or facing downwards, purplish; sepals 3-4 mm long, 1 mm broad at base, attenuate, purplish. Corolla 8-10 mm long, 15-26 mm diam., bowl-shaped; outside cream suffused with purple especially towards apices of lobes, with 5 raised longitudinal veins running down each lobe and onto tube; inside dark maroon, covered (except in lower quarter of tube) densely with low cylindrical to conical-obtuse papillae (reaching max. length in mouth of tube) each with minute apical spikelet; tube 6-8 mm deep, occupying most of flower, widening towards mouth; lobes 4-5 mm long, 5-12 mm broad at base, ascending to spreading-recurved, deltate. Corona $\pm$ 3 mm tall, 2.5-4.5 mm broad, without basal stipe; outer lobes < 1 mm long, at least partially laterally fused, with 10 obtuse lobules or nearly disc-like, spreading on base of tube but not fused to it, blackish maroon; inner lobes $\pm$ 1.0 mm long, red around base becoming blackish maroon above, adpressed to backs of anthers and exceeding them, dorsiventrally flattened, tapering from broad obtuse dorsal gibbosity at base to obtuse bristly apex.

Distribution and habitat

Huernia pendula is found in and around the gorges of the Kei and Bashee rivers in the Eastern Cape in what was formerly the Transkei. Along the Kei River it is occasional on the huge, orange sandstone cliffs around Bolo east of Stutterheim. Similar cliffs occur along

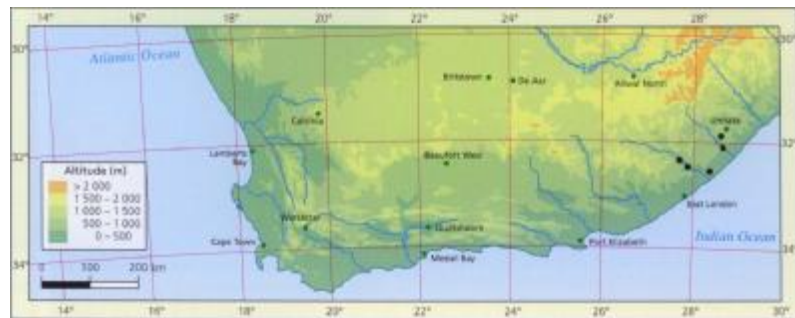


Fig. 5.31. Distribution of *Huernia pendula*.

the Bashee River in the area known as the Collywobbles and it grows there too. There is also a collection from Kentani, nearer to the sea.

Plants of *H. pendula* grow in pockets of soil and leaf-litter which gather on ledges on cliffs or on rock outcrops and they are usually found on north- or east-facing aspects.

Diagnostic features and relationships

Specimens of *H. pendula* tend to form quite densely interwoven clumps of stems with some stems hanging over the edge of ledges and becoming pendent. These pendent stems are usually not more than 300 mm long. Since they grow on the sunny and hotter sides of mountains, the clumps are frequently very exposed and can become bright pinkish. Even on young stems the tubercles are reduced to a slight swelling and rarely protrude more than 1 mm from the surface. As the stem ages they merge into the surface and are later only detectable by the small, impressed fold separating each one from the next tubercle above. The leaf-rudiment is also drastically reduced in this species and is visible only as a faint ridge on the apex of the tubercle. Consequently the stems are nearly cylindrical, resembling thick green or pinkish spaghetti. Among the Cape species

of *Huernia* this is without parallel, though this phenomenon (i.e. cylindrical stems) is found in cliff-dwelling species in other succulent groups (Taylor 1985: 62).

Most of the flowers are produced around the bases of the stems but this is variable and some even appear on the longer pendulous stems. Peduncles bear flowers over many years and can become fairly long with age. The flowers are held facing downwards, often tucked away among the stems and they may therefore be quite inconspicuous. Their inconspicuousness is heightened by the pale colour of the exterior which blends in with the colour of the stems. They are relatively small, consisting mainly of a shallowly bowl-shaped tube and short, spreading lobes around its mouth. Inside they are uniformly dark maroon and they emit an evil, excrement-like odour which is quite strong. The inside is densely covered with small papillae, each with a minute, apical bristle.

In *H. pendula* the outer corona is dark maroon like the corolla and the lobes are adpressed to the base of the tube. The inner lobes are red around their bases, becoming darker towards their tips and are short, so that they only just exceed the anthers.

Seed-horns that have been seen on *H. pendula* have generally been unusually small

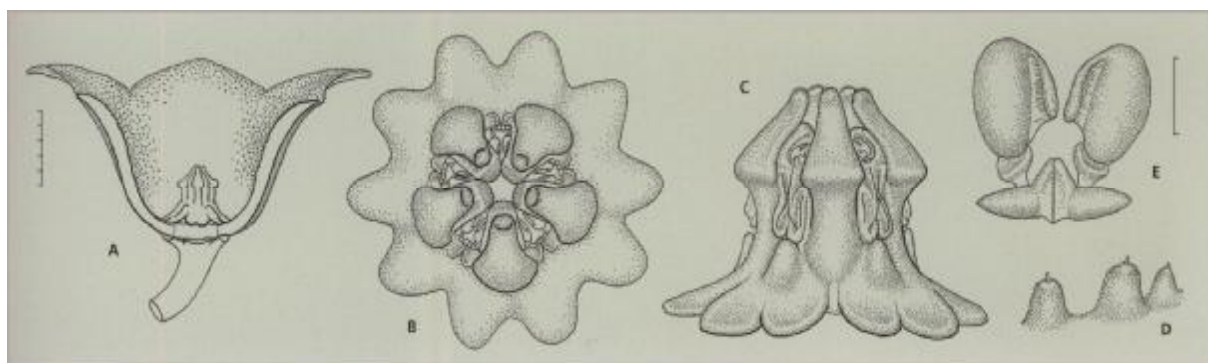


Fig. 5.32. *Huernia pendula*. A, side view of dissected flower. B, face view of gynostegium. C, side view of gynostegium. D, papillae inside corolla in mouth of tube. E, pollinarium. Scale bars: A, 5 mm; B, C, 1 mm (at E); D, 0.5 mm (at E); E, 0.25 mm. Drawn from PVB 2144, Bolo River, near Stutterheim.

HUERNIA PENDULA

(at 30-40 mm long) and contain relatively few seeds (up to 30 seeds per pair).

The flowers are not very remarkable within the genus but they share many features with species like *H. oculata* and *H. aspera*, which occur much further north. One of their interesting characteristics is the particularly short sepals and short bracts in the inflorescences. These two features and the noticeably cylindrical stems with much reduced tubercles are shared with *H. similis*, in which the flower is also similar to that in *H. pendula* both in shape and in size. There is therefore every reason to believe that these two species are closely related. This is especially remarkable since *H. similis* is only known from a small area in northern Angola, where it grows in similarly precipitous habitats in the vicinity of Pungo Andongo in Cuanza Norte province, east of the capital, Luanda.

History

According to E.A. Bruce, this remarkable species was first observed in about 1920 by a Mr. King, who kept a store at Ngwamakwe in the Transkei, east of the Kei River. The first record made was by Marjorie E.D. Courtenay-Latimer and G.G. Smith, also along the Kei River near Bolo in 1938. It seems that this species was not known at all to White & Sloane. Nevertheless, Carl Lückhoff had become aware of it and figured it in his book (Lückhoff 1952: 225), though it was at that stage still without a name and for some reason he did not give it one himself.



Fig. 5.33. *H. pendula*, PVB 2144, Bolo River, near Stutterheim.



Fig. 5.34. *H. pendula*, PVB 2144, Bolo River, near Stutterheim.



Fig. 5.35. *H. pendula*, PVB 2144, Bolo River, near Stutterheim, on sandstone cliffs above river.

7. *Huernia kennedyana*

Huernia kennedyana Lavranos, J. S. *African Bot.* 3:313(1965).

Type: South Africa, Cape, Cradock, Kennedy sub Lavranos 2356 (PRE).

Dwarf succulent forming dense mats of tightly packed stems up to 300 mm diam. Stems 10-35 mm long, 10-25 mm thick, decumbent to erect, $\pm$ globose, grey to purple-green; tubercles 1-3 mm long, low conical, abruptly narrowing into short bristle 1-2 mm long, joined into (5-) 7-9 low ridges along stem to give it tessellate appearance. Inflorescence of 1-5 flowers developing in gradual succession, arising in middle to lower half of stem on short peduncle (up to 5 mm long) with fine lanceolate bracts 1-2 mm long without lateral teeth; pedicel 4-9 (-15) mm long, 1.5 mm thick, ascending, holding flower facing upwards; sepals 3-1 mm long, 1.5 mm broad at base, ovate, acuminate. Corolla 6-8 mm long, 20-25 mm diam., shallowly bowl-shaped; outside obscurely papillate, pale pink, with 3-5 raised longitudinal veins running down lobes; inside irregularly transversely lined with red-brown to dark maroon on cream to dull yellow (lines coarsest on lobes becoming shorter and finer towards base of tube), with many terete lanceolate-obtuse to slightly clavate sometimes minutely apiculate papillae up to 3 mm long and cream suffused or dotted with reddish towards tips on lobes and for 3-5 mm into tube, below this abruptly replaced with similarly shaped but minute transparent papillae < 0.5 mm long pitering out above corona; tube 5-6 mm long, 9-10 mm broad at mouth, shallowly cupular, not pentagonal; lobes 6-8 mm long, 7-12 mm broad at base, spreading to recurved, deltate, acuminate. Corona 4.5-5.0 mm tall, 4-5 mm broad, raised above base of tube on small basal stipe; outer lobes $\pm$ 0.7 mm long, 2 mm broad, spreading parallel to base of tube and slightly above it (not fused to it), $\pm$ rectangular to slightly notched in centre, cream to pale red, raised above base of corolla on short stipe; inner lobes 2-3 mm long, yellow (slightly paler towards apices), adpressed to anthers in their lower half then rising up connivent and often diverging

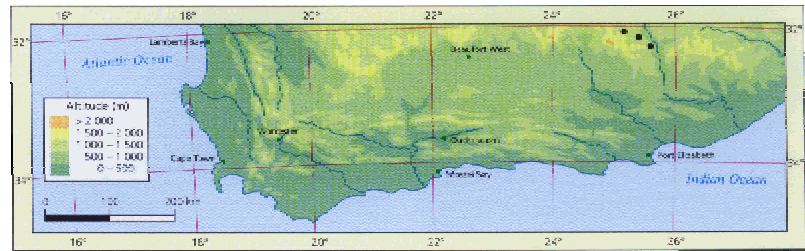


Fig. 5.36. Distribution of *Huernia kennedyana*.

towards apices, somewhat dorsiventrally flattened with swollen gibbosity at base, tapering and becoming terete above with slightly clavate finely bristly apex.

Distribution and habitat

Huernia kennedyana is known on the Great Karoo only from the area around Cradock. Plants have been found from Halesowen, which lies about 10 km south of Cradock, to about 50 km north-west of the town along the northern slopes of the Coetzeeberg and Sneeuwerge. It is thus amongst the most localised of all species of *Huernia*.

Plants have occasionally been reported from flat areas (Meve 1987). More usually they seem to be associated with slightly raised and gravelly spots. They have been seen three times on low doleritic ridges (the first was reported on in Bruyns 1982a) where the small, nearly spherical stems were often quite hard to distinguish from the little, round, dolerite pebbles between which they grew. In August 2000 a further locality was discovered and here reasonable numbers of plants of *H. kennedyana* were observed in two spots separated by about 2 km. One of these places was a low dolerite ridge as described above, while the other was

a small shale ridge where it grew in crevices among the rocks or wedged tightly among the stems of clumps of *Euphorbia ferox* or a low-growing *Sarcocaulon*.

Diagnostic features and relationships

The stems of *H. kennedyana* are ovoid to nearly spherical and, in this regard, unlike those of any other *Huernia*. The low tubercles are joined into obscure rows and this gives the stems a tessellate appearance very similar to that of *Pectinaria articulata*.

Huernia kennedyana also has an unusual and striking flower. Although the corolla is fairly small for the genus and has a relatively shallow tube with broad and short lobes, it is brightly marked inside with broken, concentric, maroon lines on a cream background. The lobes and mouth of the tube are covered with remarkably large papillae, which to some extent resemble a set of shark's teeth. These increase in size from the lobes to the mouth of the tube and then disappear abruptly just inside the mouth of the tube. They are also cream, but sometimes slightly dotted with red. There seems to be very little variation in these colours.

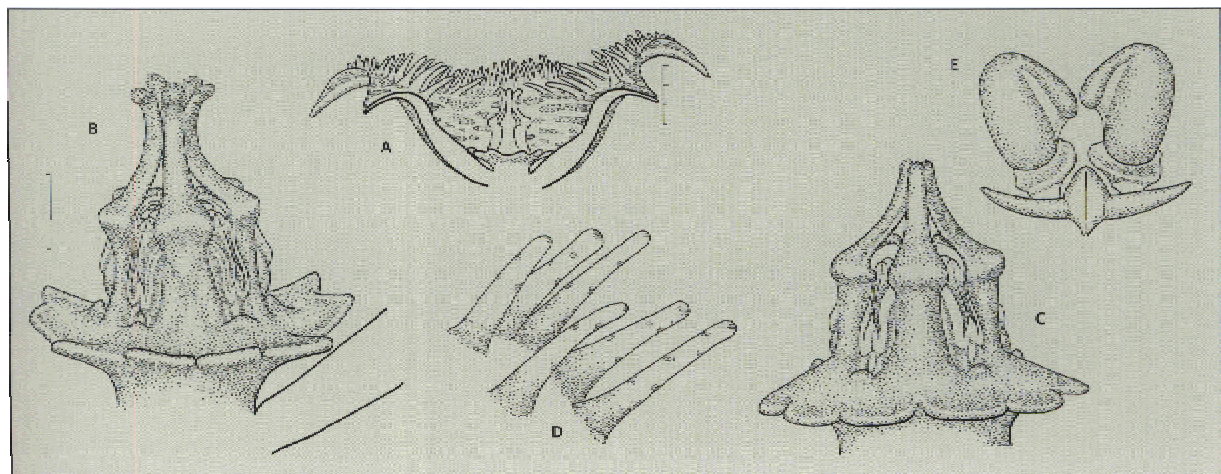


Fig. 5.37. *Huernia kennedyana*. A, side view of dissected flower. B, C, side view of gynostegium. D, papillae inside corolla in mouth of tube. E, pollinarium. Scale bars: A, 3 mm; B-D, 1 mm (at B); E, 0.25 mm (at B). Drawn from PVB 4373, north-west of Cradock.

HUERNIA KENNEDYANA

Huernia kennedyana is most unusual in that the gynostegium is raised above the base of the tube on a distinct stipe such as is mainly found in *Duvalia* and is otherwise unknown in *Huernia*. The outer corona has short lobes,

which are often cream and rather more rarely reddish. The inner lobes are longer than the anthers and form a small column in the centre. They are bright yellow.

The seed in *H. kennedyana* is unusual for

the genus in that it has a thin margin, much like that found in other stapeliads. Seedlings of *H. kennedyana* are also unconventional in that the first stems to emerge are 4-angled and usually remain so. They are usually short (up to 25 mm long) and soon give rise to lateral shoots which are mostly 5- or 6-angled. In other multi-angled species like *H. longii* and *H. pillansii* the primary stem is much longer. On it the first tubercles arise in an opposite pair and after this they rapidly increase in number to become whorled.

White & Sloane (1937) suggested originally that *H. kennedyana* may be related to *H. hystrix*. Leach (1988: 56) considered that the many-angled stems and papillate flowers suggested that *H. kennedyana* is related to *H. longii* and *H. pillansii* and maintained that the 'papillose corolla and a corona [were] somewhat reminiscent of that of *H. longii*'. He placed these three species in a series *Multangulares*. However, the small size and shallow tube of the flowers, the relatively few papillae inside the flower, the stipe beneath the gynostegium, the unusual seed and seedlings and the pale outer corona with bright yellow, relatively short inner corona lobes do not support this relationship. Consequently, in this account it is placed closer to some of the other shallow-flowered species such as *H. pendula*. However, unpublished molecular data suggest that it is probably closer to *H. pillansii* than to any other.

History

This singular species was first collected in 1931 by Hubert William 'Birdie' James (1883-1974). James was born in Watford, England. In England he suffered from respiratory problems and these caused him to come to South Africa, where he ended up settling in Cradock. At first a farm manager, he later became the branch manager of the Allied Building Society in Cradock. While in this area he became an expert on birds. He also collected plants and was particularly remarkable for having observed many stapeliads around the town, some of which were quite unusual. One of the most unusual of these was *H. kennedyana*. He sent material of this to Kirstenbosch where it was cultivated briefly and seems to have flowered rather sparingly. It is mentioned in White & Sloane (1937: 60) as '*Huernia* sp. ... with stems like a *Pectinaria* and flowers somewhat like *H. hystrix*, the spine-like fleshy papillae not as dense', which must have seemed a rather bizarre combination of characters. Nevertheless, such a thing did exist but it remained otherwise unknown until a school pupil of H.C. Kennedy brought him a single plant from his grandfather's farm north-west of Cradock in January 1964. Material from this collection was circulated in cultivation and from this it was eventually described as *H. kennedyana*.



Fig. 5.38. *H. kennedyana*, PVB 1575, south of Cradock, showing the very shallow corolla tube.



Fig. 5.39. *H. kennedyana*, PVB 4373, north-west of Cradock.



Fig. 5.40. *H. kennedyana*, PVB 4373, north-west of Cradock, more boldly marked than usual.



Fig. 5.41. *H. kennedyana*, PVB 1575, south of Cradock, in habitat, December 1977.

8. *Huernia thuretii*

Huernia thuretii F.Cels, L'Horticult. Franç.: 73, t. 3 (1866).

Stapelia thuretii (F.Cels) Croucher, Garden 12: 524 (1877).

Type: cultivated plant (missing). Lectotype: L'Horticult. Franç.: t. 3.

Huernia brevirostris N.E.Br., Gard. Chron. N.S. 7: 780 (1877).

Lectotype: South Africa, Graaff-Reinet, Bolus 575 (K, holo.; BOL, iso.).

Huernia primulina N.E.Br., Hooker's Icon. PL 20: t. 1906 (1890).

Huernia thuretii var. *primulina* (N.E.Br.) L.C.Leach, Exeelsa Taxon. Ser. 4:185 (1988).

Lectotype: Queenstown district, Barkly 13 (K).

Huernia brevirostris var. *intermedia* N.E.Br., Fl. Cap. 4(1):915(1909).

Huernia brevirostris subsp. *intermedia* (N.E.Br.) L.C.Leach, Exeelsa Taxon. Ser. 4:164 (1988).

Lectotype: Graaff-Reinet, E. Pillans sub N.S. Pillans 72 (K, holo.; BOL, iso.).

Huernia primulina var. *rugosa* N.E.Br., Fl. Cap. 4 (1): 913 (1909).

Lectotype (selected here): from a garden in Grahamstown, N.S. Pillans 43 (BOL).

Huernia scabra N.E.Br., Fl. Cap. 4 (1): 916 (1909).

Huernia brevirostris var. *scabra* (N.E.Br.) A.C.White & B.Sloane, Stap., ed. 2, 3: 872 (1937).

Type: Biesies Poort, N.S. Pillans 632 (BOL, holo.; GRA, iso.).

Huernia scabra var. *ecornuta* N.E.Br., Fl. Cap. 4 (1): 916 (1909).

Huernia brevirostris var. *ecornuta* (N.E.Br.) A.C.White & B.Sloane, Stap., ed. 2, 3: 875 (1937).

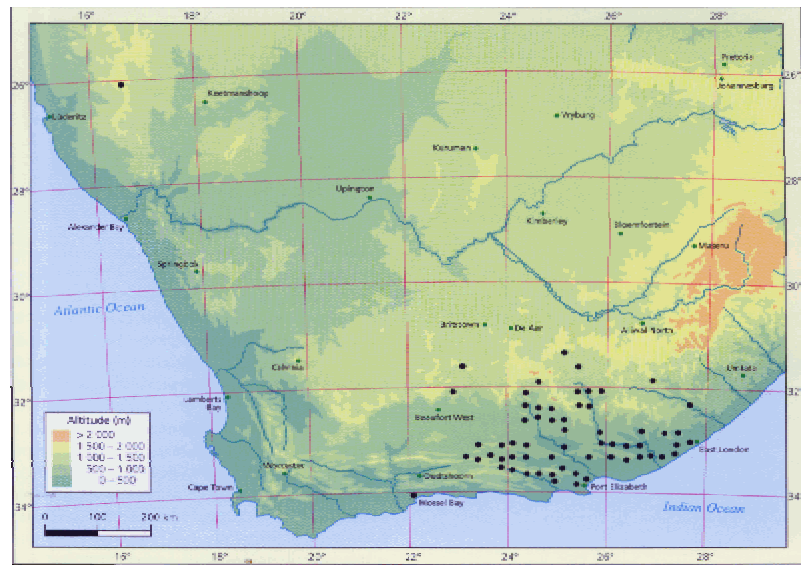


Fig. 542. Distribution of *Huernia thuretii*.

Type: Biesiespoort, N.S. Pillans 55 (BOL).

Huernia scabra var. *immaculata* N.E.Br., Fl. Cap. 4 (1): 916 (1909).

Huernia brevirostris var. *immaculata* (N.E.Br.)

A.C.White & B.Sloane, Stap., ed. 2, 3: 871 (1937).

Type: Biesies Poort, N.S. Pillans 688 (BOL).

Huernia scabra var. *longula* N.E.Br., Fl. Cap. 4 (1): 916 (1909).

Huernia brevirostris var. *longula* (N.E.Br.) A.C.White & B.Sloane, Stap., ed. 2, 3: 874 (1937).

Type: Rhenosterkop, Foster sub N.S. Pillans 140 (BOL).

Huernia scabra var. *pallida* N.E.Br., Fl. Cap. 4 (1): 916 (1909).

Huernia brevirostris var. *pallida* (N.E.Br.) A.C.White & B.Sloane, Stap., ed. 2, 3: 866 (1937).

Type: Biesies Poort, N.S. Pillans 109 (BOL).

Huernia brevirostris var. *histrionica* A.C.White & B.Sloane, Stap., ed. 2, 3:144 (1937).

Lectotype: White & Sloane, Stap., ed. 2, 3: fig. 889.

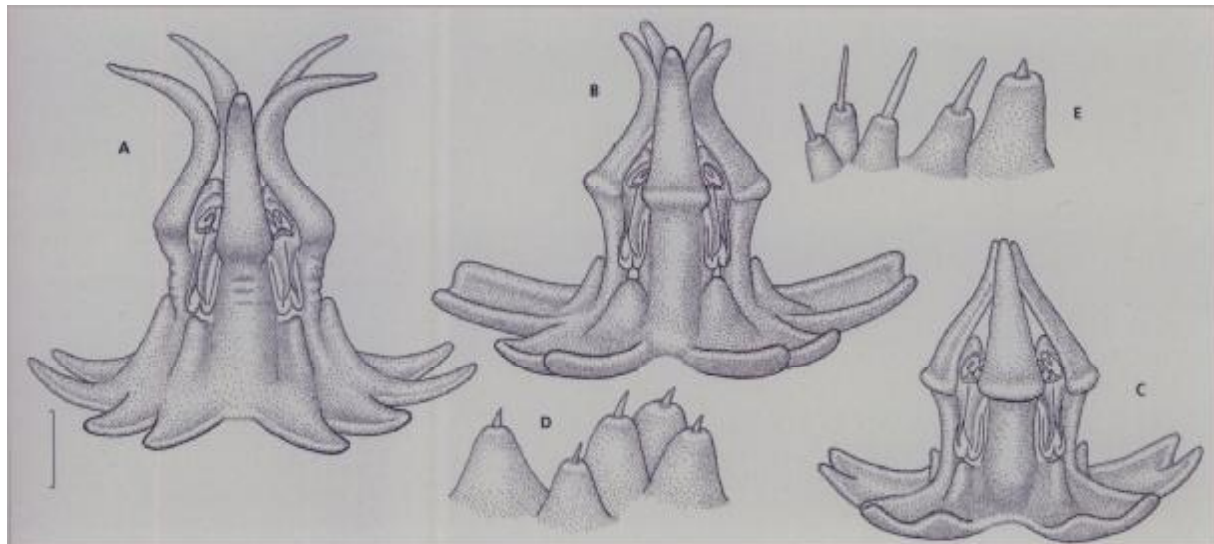


Fig. 543. *Huernia thuretii*. A-C, side view of gynoecium. D, E, papillae inside corolla in mouth of tube. Scale bars: A-C, 1 mm (at A); D, E, 0.5 mm (at A). Drawn from A, PVB, Baviaanskloof; B, D, E, PVB 4934, Sondagrivierpoort; C, PVB 5016, Keiskamma River.

HUERNIA THURETII

Huernia brevirostris var. *parvipuncta* A.C. White & B. Sloane Stap., ed. 2, 3:144 (1937).

Type: between Graaff-Reinet and Kendrew, Lückhoff 120 (missing).

Lectotype (selected here): White & Sloane, Stap., ed. 2, 3: fig. 897.

Huernia inornata Oberm. in A.C. White & B. Sloane, Stap., ed. 2, 3: 1176 (1937).

Type: Howieson's Poort, A. Wood comm. Triebner (missing).

Lectotype: White & Sloane, Stap., ed. 2, 3: fig. 122

Huernia striata Oberm. in A.C. White & B. Sloane, Stap., ed. 2, 3: 1170 (1937).

Type: Namibia, Tiras Mountains, Triebner sub Transvaal Mus. 35738 (missing).

Lectotype: White & Sloane, Stap., ed. 2, 3: fig. 1220.

Huernia bayeri L.C. Leach, *Excelsa Taxon. Ser.* 4:18 (1988).

Type: Hankey, Leach & Bayliss 15662 (NBG, holo.; PRE, iso.).

Huernia brevirostris subsp. *baviaana* L.C. Leach, *Excelsa Taxon. Ser.* 4:166-7 (1988).

Type: Baviaanskloof, Dam se Drif, Bruyns 1605 (NBG, holo.; GRA, K, M, MO, PRE, iso.).

Dwarf succulent forming dense clump 60-300 mm diam. Stems 15-60 mm long, 8-15 mm thick, decumbent, pale green to faintly mottled with reddish; *tubercles* 3-5 mm long, deltoid, spreading, laterally flattened and joined towards base into 4 (-5) angles along stem, abruptly narrowing into fine spreading acute tooth. *Inflorescences* 1-3 per stem, each of 1-10 flowers developing in gradual succession on peduncle up to 15 mm long with few narrowly acute bracts 2-4 mm long; *pedicel* 7-25 mm long, 1.5-2.0 mm thick, ascending with spreading apex holding flower facing horizontally or upwards, green to purplish; *sepals* 3-7 mm long, 1 mm broad at base, narrowly ovate-attenuate, green. *Corolla* (8-) 18-35 (-45) mm diam., rotate beyond mouth of tube to campanulate; outside smooth to somewhat irregularly roughened, cream to reddish with 1 heavy (+ 2-4 lighter) raised longitudinal veins running down each lobe; inside cream to brownish, immaculate to spotted or concentrically barred with maroon, smooth in lower half of tube, rest sometimes covered (especially towards margins of lobes) with low conical papillae at most 1 mm long (densest and longest at mouth of tube) each sometimes with apical bristle (rarely up to 2 mm long); *tube* 4-7 mm long, 6-7 mm broad at mouth, subglobose to shortly cupular and somewhat constricted at mouth by thickening of corolla, sometimes with slight annular swelling around mouth; *lobes* $\pm$ 5-8 mm long, 7-10 mm broad at base, erect to spreading, deltate, acute

to slightly acuminate. *Corona* 3.5-4.0 mm tall, 3.5-5.0 mm broad, without basal stipe; *outer lobes* triangular to subquadrate, emarginate to deeply bifid, spreading on base of tube and fused to it towards base, maroon to blackish; *inner lobes* 1.5-2.5 (-3.0) mm long, reddish to blackish, adpressed to backs of anthers for half anthers' length then ascending and connivent sometimes diverging towards apices, dorsiventrally flattened with slight dorsal gibbosity at base, tapering gradually to $\pm$ terete bristly sometimes fine apex.

The complex surrounding *H. bayeri*, *H. brevirostris*, *H. primulina* and *H. thuretii* (of Leach 1988) is very similar to that involving *Orbea variegata* or *O. lutea*. No two individuals are the same, populations exhibit an almost unbelievable range of variation and any attempt to divide them into distinct entities seems to be doomed to failure. Leach (1988) attempted this but the labyrinthine complexity of his key is ample testimony to the fact that this is a hopeless endeavour.

According to Leach (1988: 189), *H. bayeri* differs 'from all other eastern Cape Huernias in the long, simple straight hairs... in the throat and around the mouth of the tube... the presence of these hairs combined with the open campanulate corolla and long, finely subulate, widely divergent inner corona lobes is immediately diagnostic'. However, he admitted lower down on the same page that specimens of *H. thuretii* var. *thuretii* 'are sometimes a little intermediate' and plants from near Uitenhage also 'appear to be intermediate, to a slight extent, between the two taxa'. In fact, material of this collection [Leach & Bayliss 15677] deposited at BOL does not resemble *H. bayeri* at all and it has a campanulate corolla with the lobes spreading fully, in which there are almost no bristles around the mouth of the tube. In my own collection from the same area (fig. 5.50-51) some flowers had only two or three bristles in the mouth of the tube and were otherwise entirely without bristles. In addition, the inner corona lobes in *H. brevirostris* are also very often finely subulate and widely divergent (fig. 5.43 A) so it is hard to see how this character can possibly be diagnostic for *H. bayeri*.

The complexities involved in separating *H. brevirostris* and *H. thuretii* are evident already in the key (Leach 1988:16) where 'corolla lobes evidently papillate' leads to *H. brevirostris* and 'corolla smooth or with very small papillae' leads to *H. thuretii* var. *primulina*. Nevertheless (p. 185), the latter is said to have a 'much greater tendency to be papillate on the limb and lobes, sometimes quite densely and prominently'. This removes the distinction used in the key and shows that they can be very difficult, if not impossible, to separate. N.E. Brown considered *H. brevirostris* var. *intermedia* to be intermediate between *H. brevirostris* and *H. primulina* and, according to Leach (p. 166) it 'certainly appears to occupy a position between typical



Fig. 5.44. *H. thuretii*, PVB 7486, near Bathurst, flowers with an unusual, dark border.



Fig. 5.45. *H. thuretii*, PVB 7029, near Bathurst.



Fig. 5.46. *H. thuretii*, PVB 7485, near Bathurst, flowers without papillae and very attractively marked.



Fig. 5.47. *H. thuretii*, PVB 6895, near Adelaide, flowers without papillae and without markings.



Fig. 5.48. *H. thuretii*, PVB 4252, north of Klipplaat.



Fig. 5.49. *H. thuretii*, PVB 1839, about 60 km west of Patensie, Baviaanskloof.

H. brevirostris and *H. thuretii* var. *primulina*'. Indeed, Leach even annotated some specimens at NBG to the effect that he was unable to tell whether they were *H. thuretii* var. *primulina* or *H. brevirostris* subsp. *intermedia*. There seems then to be no justification for separating them under different species!

Here a broad view of this complex is taken with *H. bayeri* and *H. brevirostris* included under *H. thuretii*.

The relationships of *H. namaquensis* and *H. hallii* to this complex and to *H. nouhuysii* and *H. quinta* of much further north present a further problem. Leach (1988: 171-2) mentioned that, on the basis of morphological evidence, these two groups were most closely related to *H. brevirostris* and *H. thuretii* and that he did, at one time, consider treating them all as subspecies of a single species (p. 162). Nevertheless, he considered that they were 'satisfactorily separated by their quite different, although obviously related coronas'. However, a careful

examination of the respective coronas shows that they are all very similar. In *H. thuretii* the inner corona lobes vary from long and tapering to a slender tip to only a little longer than the anthers (fig. 5.43). In the last case they are very similar to what one finds in *H. namaquensis* and equally similar to fig. 5.70 B for *H. hallii*. I have been unable also to distinguish between the key characters (p. 20) involving the inner corona, by means of which he separated *H. namaquensis* and *H. brevirostris*. It seems that the main difference between their respective coronas lies in the length of the inner lobes: 1.5-2.5 (-3.0) mm long in *H. brevirostris*, 1.0-1.4 mm long in *H. namaquensis*. To describe the situation as involving 'quite different...coronas' is therefore a bit optimistic.

For the time being *H. namaquensis* and *H. nouhuysii* are kept separate from *H. thuretii*, despite the suggestion by Leach (1988:162,181) that they might all be treated at subspecific level within *H. thuretii*.

Distribution and habitat

Huernia thuretii has a wide distribution in the southern and Eastern Cape, from Mossel Bay to around Grahamstown and then inland into the Great Karoo around Graaff-Reinet, Cradock and Aberdeen. There are also several rather more isolated records from Biesiespoort near Victoria West. In addition, it has been gathered twice in the Tiras Mountains of southern Namibia, in an area which lies at least 800 km to the north-west of any other collection of *H. thuretii*.

Plants generally grow on stony slopes under small bushes. In the southern and eastern Cape they are mostly associated with sandstone outcrops with shallow soils on them, often in otherwise relatively moist areas, where a wide selection of other small succulents is found.



Fig. 5.50. *H. thuretii*, PVB, Groendal Dam, north of Uitenhage, flower without any papillae (some had only one or two, also 'bayeri').



Fig. 5.51. *H. thuretii*, PVB, Groendal Dam, north of Uitenhage, flowers with a few papillae in mouth of tube, each tipped with a fairly conspicuous bristle ('bayeri').



Fig. 5.52. *H. thuretii*, PVB 4939, east of Klipplaat.

HUERNIA THURETII

Diagnostic features and relationships

Plants from around Willowmore generally have a fairly short tube with the corolla spreading broadly at its mouth. This spreading area is often thickened somewhat into an annulus-like structure and beyond that the lobes spread out or may be recurved. On the inside most of the surface of the corolla is covered with papillae which are shortly cylindrical and bear a small to sometimes noticeably inflated (often dark) apical bristle. In some flowers the inside is cream with maroon spots of very variable size, some extremely fine and others rather more coarse. These spots often (but not always) tend to become narrow, broken, concentric lines in the tube and may coalesce into a maroon patch around the corona.

The opposite extreme is in the plants traditionally known under the name '*thuretii*' (figs. 5.44-46). In most of these the stems are somewhat more delicate than in '*brevirostris*' in that they are more slender and have less prominent tubercles. Plants of this kind are especially typical of small sandstone outcrops in the grassland around Grahamstown but they are also known from further to the south-west, where they were described recently as *H. bayeri*.

In these plants the corolla varies from plain cream to boldly and attractively striped with transverse maroon bars on a cream background over the whole surface, with the bars usually fusing into concentric circles in the tube and coalescing into a dark maroon patch around the corona. Here the corolla may be quite small, often as little as 18 mm in diameter, but has been recorded even down to 8 mm in the exceptional plant that was described as *H. inornata*. The corolla tube is also usually slightly constricted at the mouth and is distinctly thickened there. Papillae are mostly completely absent from the inside of the flower but, even in the area around Grahamstown, some flowers have a few, scattered papillae around the mouth of the tube.

Material described by N.E. Brown as *H. scabra*, *H. scabra* var. *immaculata* and *H. scabra* var. *pallida* from Biesiespoort near Victoria West is particularly interesting. The number of names that Brown gave to material from the same area is indicative of the variability of the plants that occur here. White & Sloane (1937) took a broad view and reduced them all to varieties of *H. brevirostris*. Leach (1988) seems to have been entirely befuddled by these collections. He noted (p. 168) that some of them had an inconspicuous annulus and some inflated bristles on the papillae inside the corolla and that these facts suggested an affinity with *H. praestans*, although the inner corona lobes were rather too short for *H. praestans*. Nevertheless, he cited one of the collections from Biesiespoort

(Pillans 55, the type of *H. scabra* var. *ecornuta*) under *H. praestans*, noting that it was aberrant or perhaps a hybrid (p. 36). My own collections from this area (figs. 5.59-60) suggest rather that White & Sloane's observation (1937) that they are connected by many intermediates to more typical '*brevirostris*' is probably the most useful and apposite and that they have nothing at all to do with *H. praestans*. The fairly prominent annular thickening around the mouth of the corolla tube in some of them is suggestive of *H. humilis*, which also occurs nearby.

History

Huernia thuretii was described by Francois Cels from cultivated plants of unknown origin and named after the algologist Gustav A. Thuret. Material known as *H. brevirostris* was discovered by Harry Bolus in April 1867 and all the plants from Biesiespoort were collected by N.S. Pillans in September 1906. The first record of material that was later called *H. bayeri* was made by Eustace Pillans in 1909 near Mossel Bay.



Fig. 5.53. *H. thuretii*, J. Bell, Oshoek, Willowmore, a plant with particularly boldly marked flowers.



Fig. 5.54. *H. thuretii*, PVB 6908, Wolfefonteinberge, Klipplaat.



Fig. 5.55. *H. thuretii*, PVB 4934, Sondagrivierpoort, Kirkwood.



Fig. 5.56. *H. thuretii*, PVB 4945, Swanepoelspoort, on this plant the bristles on the papillae were fairly long and this would have been regarded by Leach as *H. piersii*.



Fig. 5.57. *H. thuretii*, PVB 4962, east of Klaarstroom, flowers with plenty of papillae inside.



Fig. 5.58. *H. thuretii*, PVB 6314, Boesmanspoortberge, Willowmore.



Fig. 5.59. *H. thuretii*, PVB 4228, Biesiespoort. From this area N.E. Brown described several varieties of *H. scabra*.



Fig. 5.60. *H. thuretii*, PVB 4228, Biesiespoort, looking very like *H. humilis*.

9. *Huernia namaquensis*

Huernia namaquensis Pillans, J. Bot. 68:102 (1930).

Type: South Africa, Cape, gorge of Holgat River, N.S. Pillans 5155 (BOL).

Huernia herrei A.C. White & B. Sloane, Stap., ed. 2, 3:1179 (1937).

Type: South Africa, Cape, Lekkersing, *Herre* sub *Sloane* 389-1 (K).

Huernia herrei var. *immaculata* A.C. White & B. Sloane, Stap., ed. 2, 3:1180 (1937).

Type: Richtersveld, Karrachab, *Herre* (missing).

Lectotype (selected here): White & Sloane, Stap., ed. 2, 3: fig. 1228.

Huernia owamboensis R.A. Dyer, *Bothalia* 13:136 (1980).

Type: Namibia, Ovamboland (almost certainly not from this area), *Vahrmeyer* sub *PRE* 57730 (PRE).

Dwarf succulent forming dense clump 30-300 mm diam. Stems 15-40 (-60) mm long, 8-15 mm thick, decumbent, pale green to faintly suffused with reddish; *tubercles* 2-5 mm long, deltoid, spreading, laterally flattened and weakly joined towards base into mostly 5 angles along stem, abruptly narrowing into fine spreading acute tooth, somewhat flattened on upper surface. *Inflorescences* 1-3 per stem, each of 1-5 flowers developing in gradual succession on peduncle up to 15 mm long with few narrowly acute bracts 2-4 mm long; *pedicel* 7-25 mm long, 1.5-2.0 mm thick, ascending with spreading apex holding flower facing horizontally or nodding, green to purplish; *sepals* 3-7 mm long, 1 mm broad at base, narrowly ovate-attenuate, green. *Corolla* (16-) 20-30 (-35) mm diam, rotate beyond mouth of tube to campanulate; outside smooth to somewhat irregularly roughened, cream to reddish with 1 heavy (+ 2-4 lighter) raised longitudinal veins running down each lobe; inside cream, immaculate

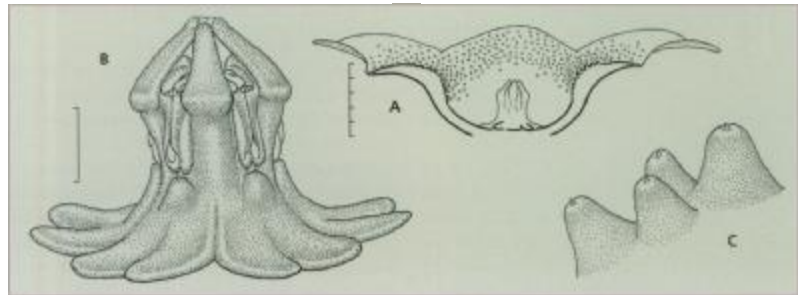


Fig. 5.61. *Huernia namaquensis*. A, side view of dissected flower. B, side view of gynostegium. C, papillae inside corolla in mouth of tube. Scale bars: A, 5 mm; B, 1 mm; C, 0.5 mm (at B). Drawn from PVB 6341, Haras Mountain, south of Anenous.



Fig. 5.62. *H. namaquensis*, PVB 4603, Komaggas, unspotted flower.



Fig. 5.63. *H. namaquensis*, Aslander 1051, Augrabies Mountain, with a coarsely spotted flower.

to finely spotted or rarely barred with maroon, smooth in lower half of tube, rest covered with low conical papillae at most 0.5 mm long (densest and longest at mouth of tube) each sometimes with minute apical bristle; *tube* 3-5 mm long, 5-7 mm broad at mouth, shortly cupular and somewhat constricted at mouth by thickening of corolla, without annular swelling around mouth; *lobes* $\pm$ 5-8 mm long, 7-10 mm broad at base, erect to spreading, deltate, acute to slightly acuminate. *Corona* 3.5-4.0

mm tall, 3.5-5.0 mm broad, without basal stipe; outer lobes subquadrate, emarginate to deeply bifid, spreading on base of tube and fused to it towards base, yellow to maroon; inner lobes 1.0-1.4 mm long, yellow sometimes with maroon markings, adpressed to backs of anthers for half anthers' length then sometimes slightly ascending and connivent, dorsiventrally flattened with slight dorsal gibbosity at base, tapering gradually to $\pm$ terete and smooth to bristly apex.

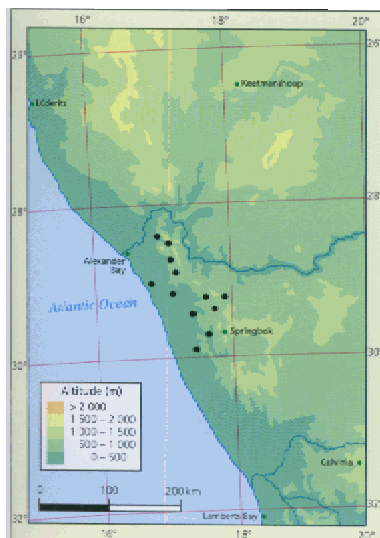


Fig. 5.64. Distribution of *Huernia namaquensis*.



Fig. 5.65. *H. namaquensis*, PVB 8259, north-east of Komaggas, in habitat, August 2000. The yellow corona lobes can just be seen in one flower and the flowers on this plant were without darker spots.

HUERNIA NAMAQUENSIS

Distribution and habitat

The only *Huernia* that is common in Namaqualand, *H. namaquensis* is found from Komaggas northwards to Hellskloof on low, dry hills and outcrops of quartzite, gneiss and schist. The records cited by Bruyns (1982b) and Leach (1988) show it to occur only as far south as a line between Port Nolloth and Steinkopf. However, it actually occurs as far south as the Kourkamma Mountain, which lies to the south of Komaggas and this is the southern limit of the kind of quartzite outcrop that it particularly favours. To the east it extends to the hills around Eenriet, north of Steinkopf, and northwards beyond Kosies.

Although regarded as very rare by H. Hall (1957), *H. namaquensis* is in fact quite common in the coastal plain of the extreme north-western Cape. Plants fill up crevices between rocks and may quite often be well hidden between and partly under rocks to escape at least partially the harsh conditions of this area.

Diagnostic features and relationships

Plants of *H. namaquensis* form dense mats of tightly packed stems. The stems are nearly always 5-angled with the tubercles not very clearly organised into rows.

The flowers of this subspecies are held somewhat away from the plant by the pedicels and face horizontally or are slightly nodding. Inside they are usually a dainty cream colour, sometimes entirely without spots but often finely spotted all over with maroon. Their interior is covered with papillae which are clearly visible to the naked eye (unlike in *H. hallii* where they are far smaller and are not easily visible).

The outer corona lobes of *H. namaquensis* are often deep maroon and in such cases they are very clearly visible against the pale inside of the flower, but they may be yellow as well, though this yellow is darker than the creamy colour inside the corolla. The inner lobes are always yellow.

History

Huernia namaquensis was described by N.S. Pillans from material that he had collected in September 1926 at the gorge of the Holgat River, to the south of Alexander Bay. These plants flowered in cultivation in his garden at Rosebank, Cape Town, in February 1928. This was, however, not the first record of this taxon. Among the illustrations made by Robert Gordon or an illustrator employed by him, there is one which almost certainly represents *H. namaquensis* (Plate 95, R.J. Gordon Collection, Rijksmuseum, Amsterdam). This figure was made during an expedition up the west coast of South Africa to the mouth of the Orange River in July and August of 1779 that was led by William Paterson. It was tentatively identified as *H. thuretii* by R.A. Dyer.



Fig. 5.66. *H. namaquensis*, PVB 6341, Harras Mountain, south of Anenous, with finely spotted flowers.

10. *Huernia hallii*

Huernia hallii E. & B.M.Lamb, *Natl. Cact. & Succ.*
J. 13: 57 (1958).

Huernia namaquensis subsp. *hallii* (E. & B.M.Lamb)
Bruyns, *Cact. & Succ. J. Gr. Brit.* 44: 86 (1982).
Neotype: Namibia, near Grünau, *H. Hall* sub NBG
511/55 (NBG).

Dwarf succulent forming dense clump 30-300 mm diam. Stems 10-25 (-30) mm long, 6-10 mm thick, decumbent, pale green to faintly suffused with reddish; *tubercles* 2-5 mm long, deltoid, spreading, laterally flattened and joined towards base into 4-5 angles along stem, abruptly narrowing into fine spreading acute tooth, somewhat flattened on upper surface. *Inflorescences* 1-3 per stem, each of 1-5 flowers developing in gradual succession on peduncle up to 15 mm long with few narrowly acute bracts 2-1 mm long; *pedicel* 7-25 mm long, 1.5-2.0 mm thick, ascending with spreading apex holding flower facing horizontally or nodding, green to purplish; *sepals* 3-7 mm long, 1 mm broad at base, narrowly ovate-attenuate, green. *Corolla* 25-38 mm diam., rotate beyond mouth of tube to campanulate; outside smooth to somewhat irregularly roughened, cream to reddish with 1 heavy (+ 2-4 lighter) raised longitudinal veins running down each lobe; inside cream, spotted and irregularly ± concentrically lined with maroon to pink, smooth in lower half of tube, rest covered with very low conical papillae at most 0.25 mm long (densest and longest at mouth of tube) each often with minute apical bristle; tube 3-5 mm long, 5-7 mm broad at mouth, shortly cupular and somewhat constricted at mouth by often considerable thickening of corolla, but without annular swelling around mouth; lobes ± 5-8 mm long, 7-10 mm broad at base, erect to spreading, deltate, acute to slightly acuminate. *Corona* 3.5-4.0 mm tall, 3.5-5.0 mm broad, without basal stipe; *outer lobes* subquadrate, emarginate to deeply bifid, spreading on base of tube and fused to it towards base, yellow to maroon; *inner lobes* 0.5-1.0 mm long, yellow, adpressed to backs of anthers for at least half length of anthers then sometimes slightly ascending and connivent, dorsiventrally flattened with slight dorsal gibbosity at base, tapering gradually to ± terete and bristly apex.

Distribution and habitat

Huernia hallii occurs in southern Namibia and is known from two areas separated by some 200 km. One of these lies in the Huib Plateau south-east of Aus, where it is found from near Aus southwards to near Witpütz. The other area is around Grünau and here it is quite common in many of the higher parts of the Great Karas Mountains to the north and north-east of this hamlet.

Plants are mainly found at altitudes of 1500-1800 m, where they form dense clumps that are tightly wedged into crevices between stones or under bushes. In the west they frequently occur on outcrops of dolomite, whereas in the Great Karas Mountains they grow on sandstones.

Diagnostic features and relationships

Specimens of *H. hallii* are densely mat-forming and often consist of very large numbers of stems. The stems are usually particularly small and are mostly less than 20 mm long. In exceptional circumstances they can reach 30 mm long and are then larger than small stems of *H. namaquensis* but this is very uncommon. They also have the characteristic reddish axillary bud above each tubercle that can be found in *H. namaquensis* (and also some other species, e.g. *H. zebrina*). The flower is usually

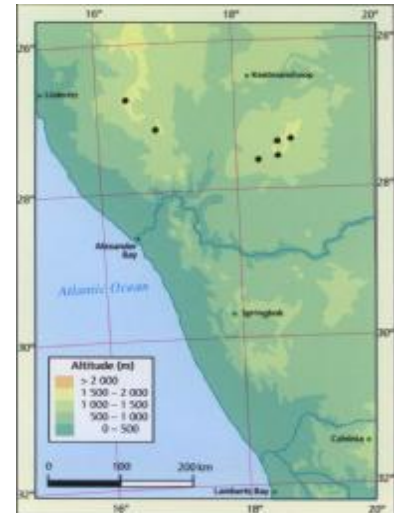


Fig. 5.67. Distribution of *Huernia hallii*.

rather flatter outside the tube than that of *H. namaquensis*, but both have a similar, nodding habit. The discovery of fairly extensive colonies in the Great Karas Mountains and the growing of many of these plants have indicated that the flowers are much more variable than was previously thought. Usually the fine spots on the inside of the flower of *H. namaquensis* are



Fig. 5.68. *H. hallii*, PVB 8341, southern Huib Plateau, Namibia.



Fig. 5.69. *H. hallii*, PVB 3529, eastern side of the Great Karas Mountains, flowers with very short transverse bars.

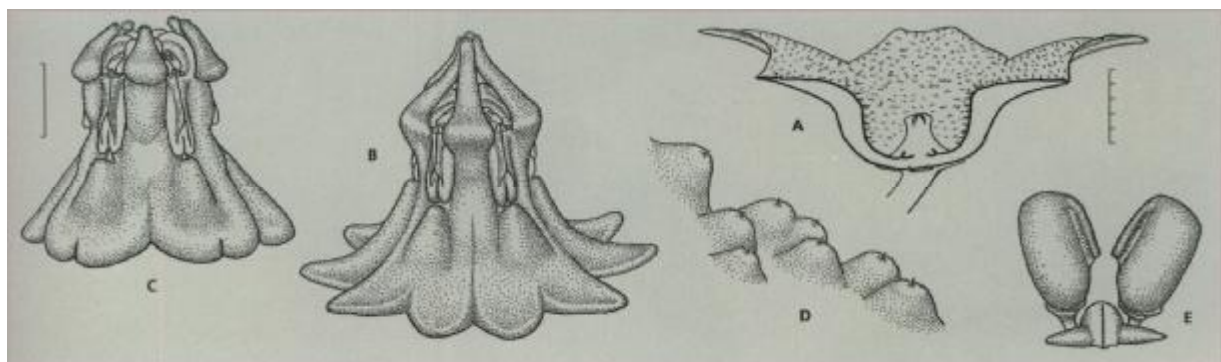


Fig. 5.70. *Huernia hallii*. A, side view of dissected flower. B, C, side view of gynostegium. D, papillae in mouth of corolla tube. E, pollinarium. Scale bars: A, 5 mm; B, C, 1 mm (at C); D, 0.5 mm (at C); E, 0.25 mm (at C). Drawn from A, B, D, PVB 3529, eastern side of the Great Karas Mountains, Namibia; C, E, PVB 5768, western side of the Great Karas Mountains, Namibia.

HUERNIA HALLII



Fig. 5.71. *H. hallii*, PVB 3529, eastern side of the Great Karas Mountains, Namibia, flowers with transverse bars.



Fig. 5.72. *H. hallii*, PVB 3529, eastern side of the Great Karas Mountains, Namibia, with finely spotted corolla.



Fig. 5.73. *H. hallii*, PVB 5791, south-western side of the Great Karas Mountains, Namibia, with a much darker colour than usual.

replaced in *H. hallii* by fine lines which often become concentric circles in the mouth of the tube. However, specimens with fine spots over the whole of the inside have also been seen. The lines may also become relatively few and coarse or may be very dense and coarse and in both cases this gives the whole flower a much darker appearance. The lower part of the tube is mostly finely spotted and there is often a dark patch around the corona. Generally the flat area beyond the tube is broader in *H. hallii* than in *H. namaquensis* so the flower is a bit larger in *H. hallii* - usually around 30 mm in *H. hallii* and around 25 mm in *H. namaquensis*.

In *H. hallii* the corona is as variable in colour as in *H. namaquensis* and, while the inner lobes are yellow, the outer lobes vary from yellow to red. Both the inner and outer corona lobes are very variable in shape. The outer lobes may be very shortly disc-like and descend steeply to the floor of the tube (as in the original collection of Hall and fig. 5.70 C) or they may be quite deeply 5-lobed and then spreading on the base of the tube. The inner lobes vary from shorter than the anthers to quite a bit longer than them, in which case they rise in the centre in a slight column (as is often seen in *H. thuretii*).

Leach (1988) maintained that the distinguishing features of *H. hallii* 'apart from the instantly recognisable stems' are: the pale green pedicel and calyx; the characteristic markings of the corolla which is 'precisely diagnostic'; the not or only slightly constricted mouth of the corolla tube; and the minute, subconical papillae on the inside of the corolla. New evidence shows that several of these characters (the colour of the pedicel and calyx, the markings inside the corolla and the shape of the corolla tube) are not diagnostic and the variation now known to occur in the colour of the corolla is shown here. This evidence now shows that the particularly small papillae on the inside of the corolla always separate *H. hallii* from *H. namaquensis* and that the generally very small stems of *H. hallii* are also almost always unequivocal. Since there is at least one character that always separates them and some other weaker distinguishing features, I have not reverted to the arrangement of two subspecies of *H. namaquensis* that I first suggested in 1982.

History

Huernia hallii was originally collected by the English horticulturist Harry Hall (1906-86), who was in charge of the succulent collection at Kirstenbosch in Cape Town from 1947 until his retirement in 1968. He first collected this species in 1955 among some quartz rocks on the flats near Grünau. It was first gathered much further to the west, near Aus, by the German botanist Otto-Heinrich Volk in 1974.

11. *Huernia nouhuysii*

Huernia nouhuysii I. Verd., Fl. Pl. South Africa 11: t. 412 (1931).

Type: South Africa, Transvaal, Soutpansberg, near Wyllie's Poort, Van Nouhuys sub PRE 8757 (missing).

Lectotype: Fl. Pl. South Africa: t. 412.

Dwarf succulent forming a dense clump 100-500 mm diam. Stems 15-60 (-200) mm long, 8-20 mm thick (excluding teeth), erect to decumbent, grey-green to purplish; tubercles 3-6 mm long, spreading, deltoid, laterally flattened towards base and joined into (4-) 5 (-6) angles usually spirally twisted along stem, tapering into stout hard acute yellowish tooth slightly flattened above. Inflorescence of 3-20 flowers developing in quick succession (often 2-3 open together), arising from short sometimes branched broad peduncle (3-25 mm long) with lanceolate bracts 2-5 mm long; pedicel 5-25 mm long, 1.5-2.0 mm thick, spreading to ascending, holding flower facing upwards or horizontally; sepals 3-8 mm long, 1.5 mm broad at base, ovate, acuminate, somewhat recurved towards apex. Corolla 18-25 mm diam., campanulate to rotate with cupular tube in centre; outside smooth, pale brown to flesh-coloured usually with 1-5 raised longitudinal veins running down centre of lobe; inside cream to white, with purple-red spots and concentric broken lines usually from tips of lobes to base of tube becoming finer in tube and coalescing into irregularly pentagonal purple-red patch around corona, covered with obtuse conical slightly dorsiventrally flattened whitish papillae (most prominent around mouth of tube where reaching 1 mm long, becoming shorter on lobes and ending abruptly just inside mouth of tube) often with apical bristle < 0.25 mm long; tube 5-8 mm long, 8-13 mm broad at mouth, cupular and slightly pentagonal, often somewhat constricted at mouth; lobes 5-6 mm long, 7-11 mm broad at base, spreading, with apices slightly recurved, deltate, acute. Corona 4-6 mm tall, 3.0-5.5 mm broad, without basal stipe; outer lobes 1-2 mm long, divided into deltoid lobules near apex to truncate and subquadrate, pale yellow suffused with pink and with maroon patch near base; inner lobes 2.0-2.5 mm long, bright yellow, below addressed to backs of

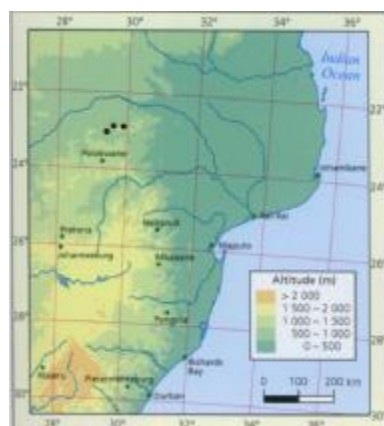


Fig. 5.75. Distribution of *Huernia nouhuysii*.



Fig. 5.74. *H. nouhuysii*, PVB 7009, near Waterpoort, Soutpansberg.

anthers and somewhat dorsiventrally flattened and broadened into transversely conspicuously gibbous base, above connivent-erect tapering slightly to obtuse slightly bristly often reddish apex.

Distribution and habitat

Huernia nouhuysii is only known from the main range of the Soutpansberg from around Wyllie's Poort westwards to near Vivo.

Plants of this species are found on rocky sandstone outcrops, usually in dry, exposed situations near the summits of the mountains, where they grow wedged in crevices or between small grass clumps. They have been seen growing with *H. whitesloaneana* in one locality and in another with two species of dwarf succulent spiny *Euphorbia*, namely *E. aeruginosa* and an especially small and slender-stemmed form of *E. griseola*.

Diagnostic features and relationships

Plants of *H. nouhuysii* are mostly quite small (< 150 mm diam.) but consist of lots of stems tightly packed together. The stems are fairly thick and short, with a distinct spiralling in the angles and they are almost always 5-angled. One of the unusual features of the stems is the rudimentary leaves which (while they are still green) are conspicuously flattened above and have a broadened base. These rapidly dry off into a sometimes sharpish, spine-like tooth which gradually wears down to leave a hard, greyish cap over each tubercle.

The somewhat foul-smelling flowers are produced in quite dense clusters and seem to follow each other in quick succession, often with two or three open simultaneously in one inflorescence. They are extremely variable in

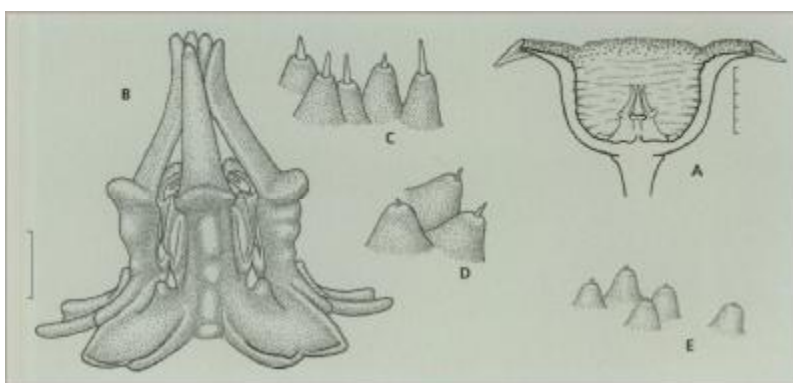


Fig. 5.76. *Huernia nouhuysii*. A, side view of dissected flower. B, side view of gynostegium. C-E, papillae inside corolla in mouth of tube. Scale bars: A, 5 mm; B, 1 mm; C-E, 0.5 mm (at B). Drawn from: A,E, PVB 7009, near Waterpoort, Soutpansberg; B-D, PVB 6584, near Vivo, Soutpansberg.

HUERNIA QUINTA

shape: some have very short lobes at the mouth of the tube while others have a slight flattish area beyond the tube before the lobes begin. The colour inside is not nearly so variable and most of them are prettily flecked with spots and transverse lines of purple-red on cream to whitish. The papillae on the inside may be densely packed to quite sparse and have only a short apical bristle.

One of the most striking features of the flower in *H. nouhuysii* is the brilliant yellow inner corona lobes. There are often a few sizeable purple or maroon spots just below their dorsal gibbosities. The outer lobes are much less noticeable, being pale yellow with a few maroon bands and often with a maroon margin. Consequently they are fairly inconspicuous against the background colour of the base of the corolla tube. They usually have a particularly prominent tubercle just below the guide-ribs.

There is a surprising degree of correspondence between *H. nouhuysii* and *H. quinta*. Plants in both species have mostly 5-angled stems with stout, yellow-tipped and somewhat hardened teeth along the stems, the flowers are borne in clusters on a relatively thick peduncle and in both several flowers often open at once. The main differences between them are the shorter corolla lobes, the almost total lack of a flattened area around the mouth of the tube and below the lobes, the manner in which the broader, dark markings on the corolla continue to the tips of the lobes, the shorter apical bristles on the papillae, and the longer inner corona lobes in *H. nouhuysii*.

Huernia nouhuysii is more obviously different from *H. blyderiverensis*. The latter has 4-angled stems, which lack the somewhat hardened teeth along the stems and the flowers are much broader. The papillae inside the corolla are similar to those of *H. nouhuysii*. A further difference between them is found in the follicles. These are relatively short (< 80 mm long) and stout and brightly marked with



Fig. 5.77. *H. nouhuysii*, PVB 6584, near Vivo.

longitudinal stripes in both *H. nouhuysii* and *H. quinta*. In *H. blyderiverensis* they are longer (usually 100-120 mm long) and more slender and are without markings.

Huernia quinta was originally described as a variety of *H. scabra*, which is now a synonym of *H. thuretii*. It is possible that *H. nouhuysii* should also be a synonym of *H. thuretii* but, for the present, this change is not made. The three species *H. blyderiverensis*, *H. nouhuysii* and *H. quinta* are mainly distinguished from the members of the complex around *H. thuretii* by the dense inflorescences on which the flowers develop in rapid succession, so that there are often several flowers open simultaneously on each peduncle. An additional difference is the bright yellow inner corona lobes which are present in all three but are never found in *H. thuretii*. Of these three species, *H. blyderiverensis* is the most similar to plants in the *H. thuretii* complex, with its 4-angled stems and relatively broad corolla.

History

Huernia nouhuysii was discovered by Jan J. van Nouhuys in the Soutpansberg just before 1931. Very few collections have been made of it and all were from near the type locality. Only recently it has been shown to be much more widespread in these mountains, though it has not, as yet, been found in the Blouberg, nor is it known anywhere to the east of Wyllie's Poort.



Fig. 5.78. *H. nouhuysii*, PVB 6584, near Vivo, Soutpansberg.

12. *Huernia quinta*

Huernia quinta (E.Phillips) A.C.White & B.Sloane, *Stap.*, ed. 2, 3: 885 (1937).

Huernia scabra N.E.Br. var. *quinta* E.Phillips, *Fl. Pl. South Africa* 12: t. 444 (1932).

Type: South Africa, of unknown origin, Van Balen sub PRE 10134 (PRE).

Dwarf succulent forming a dense clump up to 300 mm diam. or more. Stems 15-60 (-200) mm long, 8-20 mm thick (excluding teeth), erect to decumbent, grey-green to purplish; *tubercles* 3-6 mm long, spreading, deltoid, laterally flattened towards base and joined into (4-) 5 (-6) angles often spirally twisted along stem, tapering into stout hard acute yellowish tooth slightly flattened above. *Inflorescence* of 3-20 flowers developing in quick succession (often 2-3 open together), arising from short sometimes branched broad peduncle (3-25 mm long) with lanceolate bracts 2-5 mm long; *pedicel* 5-25 mm long, 1.5-2.0 mm thick, spreading to ascending, holding flower facing upwards or horizontally; *sepals* 3-8 mm long, 1.5 mm broad at base, ovate, acuminate, somewhat recurved towards apex. *Corolla* (20-) 25-30 (-40) mm diam., campanulate to rotate with cupular tube in centre; outside smooth, pale brown to flesh-coloured or green usually with 1-5 raised longitudinal veins running down centre of lobe; inside pale cream to white (sometimes faintly pinkish or greenish towards edges of lobes), with narrow often concentric pentagonal maroon lines in and around mouth of tube (rarely on lobes) shortening to elongated spots in tube and coalescing into irregularly pentagonal purple-red patch around corona, covered with obtuse conical slightly dorsiventrally flattened whitish papillae (most prominent around mouth of tube where reaching 1 mm long, becoming shorter on lobes and ending abruptly just inside mouth of tube) with fine dark maroon apical bristle up to 1 mm long; *tube* 6-9 mm long, 7-10 mm broad at mouth, cupular and slightly pentagonal, often somewhat constricted at mouth; *lobes* 7-11 mm long, 10-15 mm broad at base, spreading, with apices slightly recurved, deltate, acute. *Corona* 4-6 mm tall, 3.0-5.5 mm broad, without basal stipe; *outer lobes* 1-2 mm long, divided into deltoid lobules near apex to truncate and subquadrate, pale

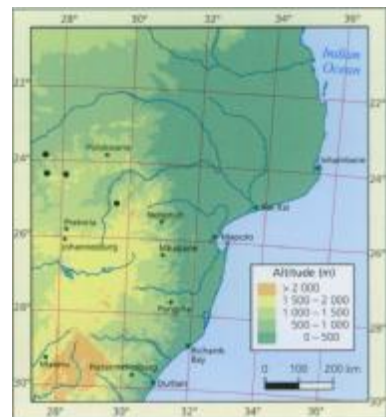


Fig. 5.79. Distribution of *Huernia quinta*.

yellow suffused with pink and with maroon patch near base; inner lobes 1.0-1.5 mm long, bright yellow, below adpressed to backs of anthers and somewhat dorsiventrally flattened and broadened into transversely slightly gibbous base, above connivent-erect tapering slightly to obtuse slightly bristly often reddish apex.

Distribution and habitat

Huernia quinta is widely and sporadically distributed in the northernmost part of South Africa, from Ellisras, slightly west of the Waterberg, through the Waterberg to Groblersdal.

In the Waterberg and around Ellisras plants grow in exposed spots with shallow soils among sandstone outcrops whereas near Groblersdal it occurs among grasses and a few other succulents on granite outcrops.

Diagnostic features and relationships

In *H. quinta* the plant can form a large clump of densely packed stems. The stems are identical to those of *H. nouhuysii*, that is, comparatively thick and short with distinctly spiralling angles and with fairly hard teeth along them. They are almost always 5-angled, though occasional plants can be found where 4-angled stems predominate.

The flowers of *H. quinta* are quite remarkably beautiful. The outside of the buds may become quite dark flesh-coloured just before they open. On the inside the corolla is adorned with narrow, broken, concentric, maroon lines on an otherwise almost wholly white background. The lines are longest at the mouth of the tube and usually fade out just beyond the mouth. In the tube they become shorter and change to spots in the lower half. There is often a plain white patch near the base of the tube before the rather irregular, shiny, maroon patch around the corona. This, with the pale patch on the outside of the flower towards the base lets in more light at the base of the tube and has somewhat of a window effect. The



Fig. 5.80. *H. quinta*, PVB 7780, along Bulge River, Waterberg. A large specimen growing in very shallow soil on a flat, sandstone outcrop, January 1999.

flowers emit a faint, but noticeably bad, excrement-like odour.

The papillae on the inside of the corolla are usually adorned with apical bristles which may reach 1 mm long and may be maroon (and then quite obvious). However, the bristles are quite variable in length and may be scarcely visible in some flowers.

In *H. quinta* the outer corona is white and somewhat translucent towards the tips, so it is barely distinguishable from the base of the corolla tube. As in *H. nouhuysii*, the inner corona lobes are bright yellow and therefore quite obvious in the centre of the flower.

History

This species was originally described in 1932 by E.P. Phillips as a variety of *H. scabra*, which is now regarded as synonymous with *H. thuretii*. The material from which it was described was taken from the garden of Jan C. van Balen but appears to have been collected about 20 miles south of Ellisras (Leach 1988), where it still grows together with *Euphorbia tortirama*.



Fig. 5.81. *H. quinta*, PVB 7780, along Bulge River, Waterberg.



Fig. 5.82. *H. quinta*, Peckover, Palmietfontein, Waterberg.

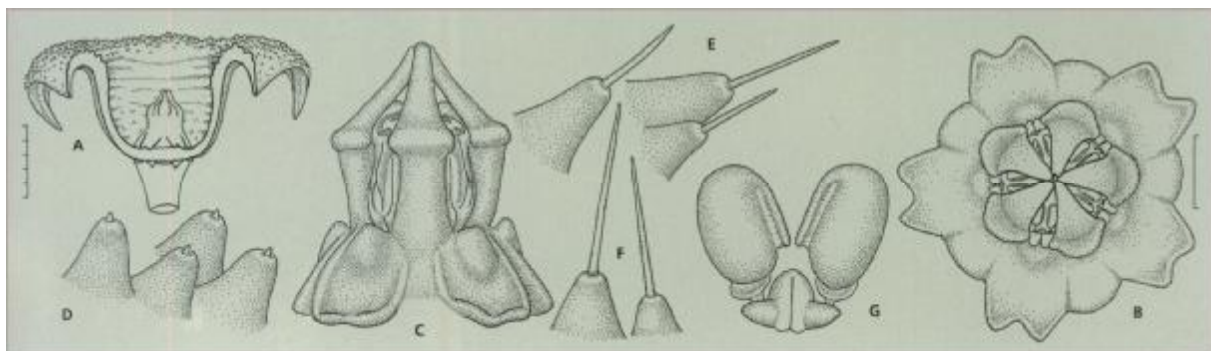


Fig. 5.83. *Huernia quinta*. A, side view of dissected flower. B, face view of gynostegium. C, side view of gynostegium. D, papillae inside corolla just beyond mouth of tube. E, F, papillae below mouth of corolla tube. G, pollinarium. Scale bars: A, 5 mm; B, C, 1 mm (at B); D-F, 0.5 mm (at B); G, 0.25 mm (at B). Drawn from A, C-E, G, PVB 6622, northeast of Groblersdal; B, R PVB 7780, along Bulge River, Waterberg.

HUERNIA BLYDERIVERENSIS

13. *Huernia blyderiverensis*

Huernia blyderiverensis (L.C.Leach) Bruyns,
comb. et stat. nov.

Huernia quinta var. *blyderiverensis* L.C.Leach,
Exceisa Taxon. Ser. 4:178 (1988).

Type: South Africa, Transvaal, along Ohrigstad
River, Percy-Lancaster 466 (NBG).

Dwarf succulent forming a dense clump up to 300 mm diam. or more. Stems 15-60 (-200) mm long, 8-20 mm thick (excluding teeth), erect to decumbent, grey-green to purplish; *tubercles* 3-6 mm long, spreading, deltoid, laterally flattened towards base and joined into 4 (-5) wing-like and straight angles along stem, tapering into soft point soon wearing away but slightly flattened above. *Inflorescence* of 3-20 flowers developing in quick succession (often 2-3 open together), arising from short sometimes branched broad peduncle (3-25 mm long) with lanceolate bracts 2-5 mm long; *pedicel* 5-25 mm long, 1.5-2.0 mm thick, spreading to ascending, holding flower facing upwards or horizontally; *sepals* 3-8 mm long, 1.5 mm broad at base, ovate, acuminate, somewhat recurved towards apex. *Corolla* 25-35 (-45) mm diam., campanulate to rotate with cupular tube in centre; outside smooth, pale brown to flesh-coloured or green usually with 1-5 raised longitudinal veins running down centre of lobe; inside white, with purple-red spots and narrow concentric broken lines sometimes on lobes and around mouth of tube and always with elongated spots towards base of tube coalescing into irregularly pentagonal purple-red patch around corona, covered with obtuse conical slightly dorsiventrally flattened whitish papillae (most prominent around mouth of tube where reaching 1 mm long, becoming shorter on lobes and ending abruptly just inside mouth of tube) often with apical bristle < 0.25 mm long; *tube* 6-9 mm long, 7-10 mm broad at mouth, cupular and slightly pentagonal, often somewhat constricted at mouth; *lobes* 8-13 mm long, 10-15 mm broad at base, spreading with

apices slightly recurved to reflexed, deltate, acute. *Corona* 4-6 mm tall, 3.0-5.5 mm broad, without basal stipe; *outer lobes* 1-2 mm long, divided into deltoid lobules near apex to truncate and subquadrate, pale yellow suffused with pink and with maroon patch near base; *inner lobes* $\pm$ 1.5 mm long, bright yellow, below adpressed to backs of anthers and somewhat dorsiventrally flattened and broadened into transversely conspicuously gibbous base, above connivent-erect tapering slightly to obtuse slightly bristly often reddish apex.

Distribution and habitat

Huernia blyderiverensis is found from Kromellenboog among the hills along the southern banks of the Olifants River to the slopes of the mountains overlooking the Blyde River. It seems to occur only on dolomite, in shallow soils on ledges and outcrops of rock.

Plants grow in extraordinary abundance in places, with a profusion of other succulents. These include *Orbea gerstneri*, *Brachystelma parvulum*, *Euphorbia lydenburgensis* and another smaller species of *Euphorbia*.

Diagnostic features and relationships

Plants of *H. blyderiverensis* may form very large clumps up to 300 mm in diameter. The 4-angled stems are usually somewhat more loosely packed into these clumps than they are in *H. quinta*.

Huernia blyderiverensis is just as prettily flowered as *H. quinta* and has turned out to be extremely variable in the colour of the flowers. Again the inside of the flower is mostly white and against this background there are usually maroon lines or spots. These maroon markings

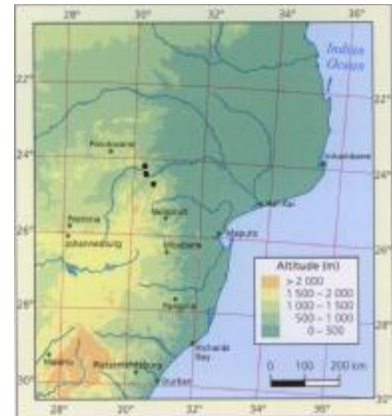


Fig. 5.84. Distribution of *Huernia blyderiverensis*.

are occasionally restricted to the tube as small elongated spots but equally well they may be concentric, broken lines (as in *H. quinta*) which peter out beyond the mouth of the tube. Specimens have even been seen where the broken lines continue to the tips of the lobes (fig. 5.88), as is the case in *H. nouhuysii*. The united area outside the tube and below the lobes is usually quite flat or even sometimes somewhat reflexed. It is generally considerably broader than is found in either *H. nouhuysii* or *H. quinta*. The inside of the corolla is also covered with papillae, each of which has a very short apical bristle, often with a maroon spot surrounding its base. As is usual, these papillae mostly end off abruptly just inside the mouth of the tube, though in this species there are sometimes odd

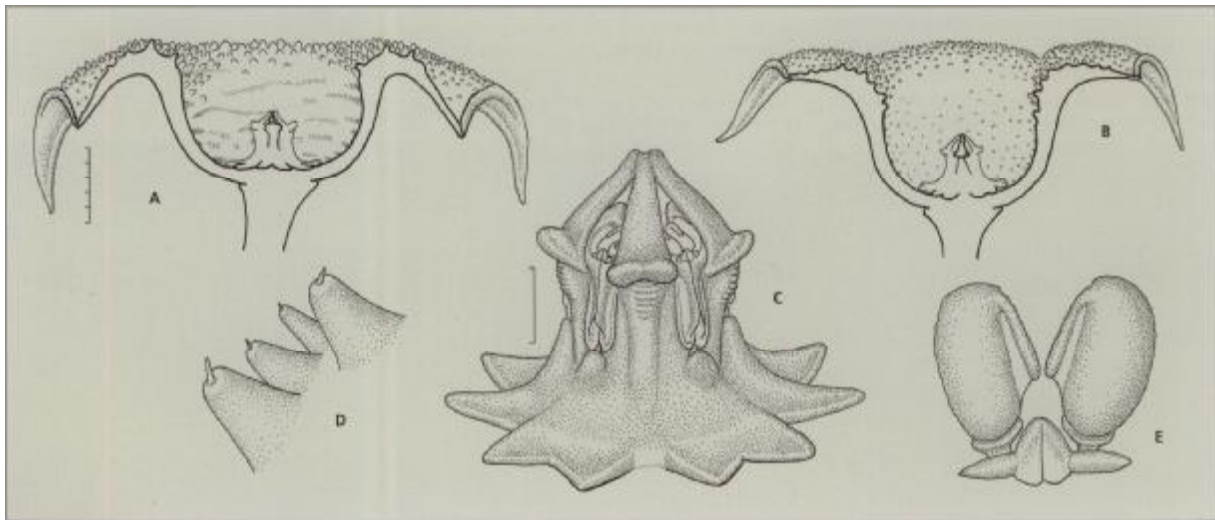


Fig. 5.85. *Huernia blyderiverensis*- A, B, side view of dissected flower. C, side view of gynostegium. D, papillae inside corolla in mouth of tube. E, pollinarium. Scale bars: A, B, 5 mm (at A); C, 1 mm; D, 0.5 mm (at C); E, 0.25 mm (at C). Drawn from A, C-E, PVB 6619, Kromellenboog, Olifants River; B, PVB 6600, north-east of Ohrigstad.



Fig. 5.86. *H. blyderiverensis*, PVB 6619, Kromellenboog, Olifants River.



Fig. 5.87. *H. blyderiverensis*, PVB 6619, Kromellenboog, Olifants River.



Fig. 5.88. *H. blyderiverensis*, PVB 6600, north-east of Ohrigstad, flowers with transverse stripes nearly to tips of lobes.

scattered papillae and even scattered bristles on the corolla tube around the corona. The flowers emit a faint bad odour.

In *H. blyderiverensis* the outer corona lobes are white with patches of maroon towards their margins and the inner lobes are a striking yellow, occasionally with some maroon markings.

Leach (1988) stated that his 'var *blyderiverensis*' 'differs from the typical variety in its spotted, not at all transversely striped larger corolla...and the tube markedly constricted at the mouth'. The photographs shown here

demonstrate that the lack of transverse stripes cannot be used to separate them since they are actually found in both. The tube in both his varieties is usually 'markedly constricted at the mouth' so this, too, is not a useful criterion. The data that are now available show that *H. blyderiverensis* is distinguished from *H. quinta* by the mainly 4-angled stems without the hardened tips to the tubercles, the considerably broader flat area outside the corolla tube and below the lobes, and the particularly short, apical bristles on the papillae inside the corolla around the mouth of the tube.

History

This species seems to have been observed and collected for the first time by Alan Percy-Lancaster (1944-95) in about 1975. My own collections, that have been made since 1996, have somewhat extended the known distribution to the valley of the Olifants River. Leach (1988) treated this species as a variety of *H. quinta*. However, it differs from *H. quinta* in several features and there is reason to believe that it is, it anything, closer to members of the complex surrounding *H. thuretii*. Consequently it is treated here as a separate species.



Fig. 5.89. *H. blyderiverensis*, PVB 6600, north-east of Ohrigstad, in habitat, January 1997, flowers with transverse stripes only inside corolla tube.

HUERNIA HUMILIS

14. *Huernia humilis*

Huernia humilis (Masson) Haw., *Syn. Pl. Succ.* 30 (1812).

Stapelia humilis Masson, *Stap. Nov.* 10, t. 5 (1796).

Type: South Africa, Cape, Masson (missing).

Lectotype: Masson, *Stap. Nov.* t. 5.

Huernia simplex N.E.Br., *Fl. Cap.* 913 (1909).

Lectotype: Victoria West division, Thomson sub

Galpin 3056 (K, holo.; BOL, PRE, iso.).

H. thudichumii L.C. Leach, *Excelsa Taxon. Ser.* 4:132 (1988).

Type: Klaarstroom, *Thudichum* 214A (NBG).

Dwarf succulent forming dense clump up to 300 mm diam. *Stems* (10) 20-30 (-40) mm long, 8-20 mm thick (excluding teeth), erect, short and stout often somewhat pyramidal, grey-green occasionally marked with purple; *tubercles* 2-4 mm long, broadly deltoid, spreading, laterally flattened and joined into 4 (-5) angles along stem, tapering to small acute teeth. *Inflorescence* of 1-5 flowers developing in gradual succession, arising near base of stem from short peduncle (up to 5 mm long) with fine lanceolate bracts $\pm$ 2 mm long without lateral teeth; *pedicel* 10-18 mm long, 1.5-2.0 mm thick, ascending then spreading usually holding flower facing horizontally (sometimes upwards); *sepals* 2.5-5.0 mm long, 1.5-2.0 mm broad at base, ovate, acuminate. *Corolla* 25-40 (-45) mm diam., rotate; outside smooth, cream with 1 heavy (+ 2 fainter) raised longitudinal veins running down centre of each lobe; inside cream often faintly speckled with red and more densely blotched with red or maroon on raised slightly shiny annulus to plain red or maroon in tube, occasionally wholly cream, with minute papillae on lobes each with shortly acute rather swollen maroon-tipped apical bristle, sometimes with few stiff slightly clavate dark maroon bristles 1-3 mm long in mouth of tube; *tube* 4-5 mm long, 6-8 mm broad at mouth, cupular, only slightly to clearly pentagonal, mouth formed by raised annulus (annulus only slightly thickened and forced upwards by strong reflexion of corolla below bases of lobes); *lobes* 10-12 mm long, 9-17 mm broad at base, spreading to reflexed, $\pm$ deltate, acute. *Corona* $\pm$ 3.0 mm tall, 2.5-4.0 mm broad, without basal stipe; *outer lobes* 0.5-1.0 mm long, dark maroon, shortly and obtusely bilobed, spreading to touch base of

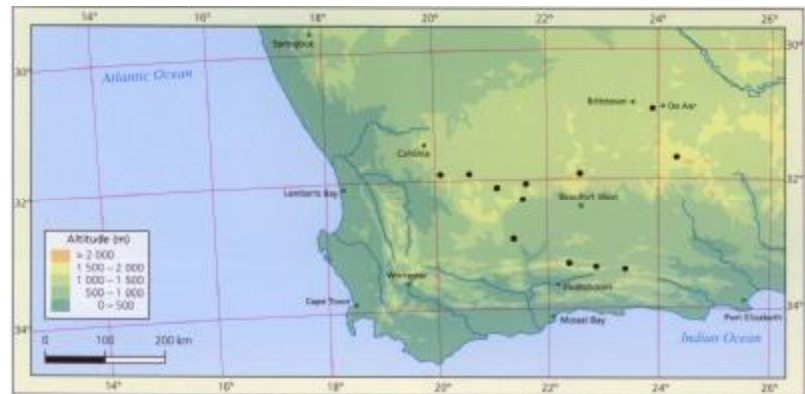


Fig. 590. Distribution of *Huernia humilis*.

tube but not fused to it; *inner lobes* 0.7-1.0 mm long, maroon to orange, adpressed to backs of anthers, shorter than to exceeding them, tapering from broad transverse dorsal gibbosity to small bristly acute apex.

Distribution and habitat

Exploration over the last ten years has shown that *H. humilis* is widespread in the Great Karoo from Prince Albert and Willowmore to Beaufort West, Richmond, De Aar and westwards to Middelpos. As it is quite common in some areas, it is not the extreme rarity that it was once thought to be and its apparent rarity is only a reflection of the paucity of collecting in these areas.

Plants usually grow wedged in crevices among dolerite or metamorphosed shale rocks, sometimes under small bushes but often in the open.

Diagnostic features and relationships

According to Leach (1988) there are five species in southern Africa which have what appears to

of the tube and relatively short inner corona lobes only just exceeding the anthers. These are *H. humilis*, *H. insigniflora*, *H. plowesii*, *H. thudichumii* and *H. zebrina*, and there are two (*H. laevis* and *H. somaica*) in north-eastern Africa and Arabia. The last two differ from the southern African ones in that they have fairly prominent papillae on the corolla lobes. *Huernia insigniflora* and *H. zebrina* differ from the other three (*H. humilis*, *H. plowesii*, *H. thudichumii*) in southern Africa by having variously transversely striped corolla lobes (the lobes are spotted in the others) with slender and spike-like apical bristles on the tiny papillae on the lobes. In the other three southern African taxa the papillae on the lobes are equally tiny but their apical bristle is shortly acute and often shaped like an inverted top.

Huernia humilis is more than usually variable in the colour of the inside of the flowers, though the variation is similar to that in the expanded concept of *H. zebrina* presented here. There is much variation (as is to be expected) in the size and frequency of the red spots on the lobes and some more densely spotted flowers even have a small

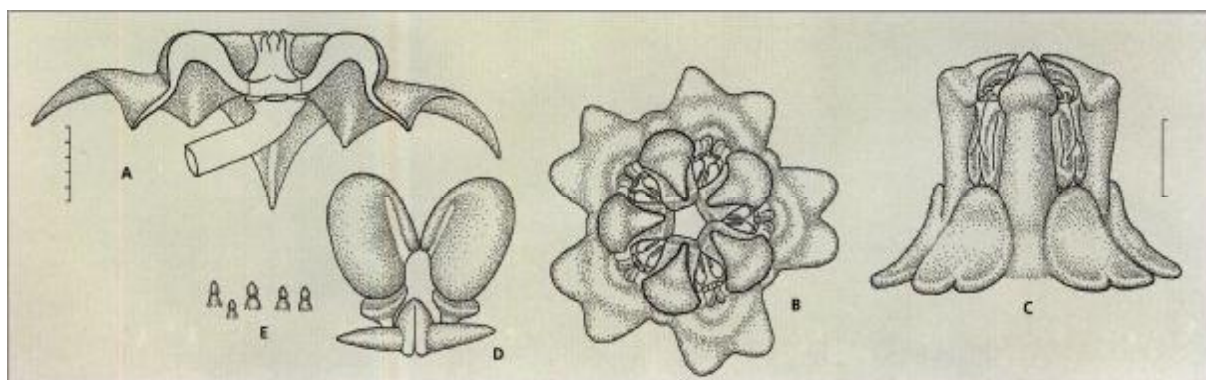


Fig. 591. *Huernia humilis*. A, side view of dissected flower. B, face view of gynostegium. C, side view of gynostegium. D, pollinarium. E, papillae inside corolla on lobes. Scale bars: A, 5 mm; B, C, 1 mm (at C); D, 0.25 mm (at C); E, 0.5 mm (at C). Drawn from PVB 4816, south-east of Fraserburg.



Fig. 5.92. *H. humilis*, PVB 5971, south-west of Fraserburg, in habitat, April 1994.



Fig. 5.93. *H. humilis*, PVB 4816, south-east of Fraserburg.



Fig. 5.94. *H. humilis*, Heunis, Middelpas. Here the corolla tube is quite clearly pentagonal.



Fig. 5.95. *H. humilis*, PVB 6636, south of De Aar, with bristles around the mouth of the corolla tube.



Fig. 5.96. *H. humilis*, PVB 4958, east of Klaarstroom. This corresponds to material known as *H. thudichumii*. Here there is also sometimes a faint mottling of red on the corolla and the tube is faintly suffused with pink.



Fig. 5.97. *H. humilis*, PVB 6669, south of Victoria West, a flower with much less red on it than normal.

reddish patch at the tips of the lobes. More significant, though, is that I have found some populations near Victoria West where there is a range of colours from spotted with red all over (coalescing towards the mouth of the tube) to spotted only around the mouth of the tube (plain red inside it), with the rest of the flower uniformly cream. Since *H. thudichumii* differs from *H. humilis* only in the colour of the flowers (they were given as uniformly 'ivory-coloured' and rarely 'obscurely marked with pale pinkish spots', Leach 1988:133), some of these flowers from Victoria West are indistinguishable from those of *H. thudichumii*. There is therefore no reason to maintain this as a distinct species from *H. humilis*.

According to Leach (1988) *H. plowesii* differs from all other members of his series *Humiles* by the 'long stiff hairs of the throat and annulus' as well as 'the somewhat constricted mouth of the distinctly pentagonal tube'. The position is not quite as clear as he suggested, however, since in some flowers of *H. plowesii* there are only 7-12 bristles in the mouth of the tube (e.g. PVB 5731) and in a few collections of *H. humilis* (notably from south-east of De Aar, PVB 6636) there are 10-15 such bristles in the mouth of the tube also. Furthermore, in most of the flowers seen of *H. humilis* the tube is obscurely pentagonal to nearly cylindrical but some have been collected where the tube is distinctly pentagonal (fig. 5.94). For *H. plowesii* he also mentioned the 'acute pubescence of the [inside of the] corolla lobes which is quite different from that of *H. humilis* which is almost

papilla-like'. Variation has been seen in this feature too, with some of the apical bristles on these minute papillae very similar to those of *H. humilis*. Material seen subsequent to Leach's revision therefore shows that all the differences found by Leach between the two species are weak. Nevertheless, because of the considerable disjunction in their distributions, *H. plowesii* is still recognised at specific level here.

The plant in *H. humilis* forms a very dense

clump of 4-angled stems, which are usually short and squat and often broader than tall. The flowers in this species are very pretty. On the inside the lobes are finely spotted with red on a cream background with the spots increasing in size and coalescing on the annulus to become plain red towards the mouth of the tube. The annulus is never as shiny and the colours are generally not as bold as in *H. zebrina*. As mentioned above, the inside of



Fig. 5.98. *H. humilis*, PVB 6669, south of Victoria West. In this plant the red colouring on the corolla is restricted to the tube and the flower begins to resemble that in *H. thudichumii*. Some of these flowers also had a few bristles in the mouth of the tube.

HUERNIA PLOWESII

the lobes is covered with fine papillae whose apical cell is swollen into a shortly acute, top like structure which is usually maroon. These papillae are mainly concentrated on the cream parts of the lobes, with the red blotches mostly free of them. They usually disappear towards the bases of the lobes.

As in *H. zebrina*, the corolla in *H. humilis* is strongly reflexed just below the bases of the lobes. This often accentuates the annulus so that it stands out well above the lobes as a thick, inflated ring. If the flower is dissected, it is found that the corolla reaches a maximum of about twice as thick in this annulus as it is below it and so the main cause of the prominence of the annulus is the manner in which the corolla is reflexed around the mouth of the tube. This annulus is very variable in its prominence and in some flowers it is almost absent. In such cases the flower begins to resemble that of some forms of *H. thuretii*. This is especially similar to what is found in plants that were described as *H. scabra* var. *ecornuta* from Biesiespoort near Victoria West. In these plants there is a fairly prominent annulus around the mouth of the tube and the flower is fairly boldly spotted with red (fig. 5.59-60). More similar to *H. thuretii* is the presence in these flowers of papillae with tiny apical bristles around the mouth of the tube. There is, therefore, some evidence to suggest that *H. humilis* and *H. thuretii* intergrade and this deserves further investigation.

History

Huernia humilis was first collected by Francis Masson before 1796. It is not at all clear that his figure of *Stapelia humilis* represents what is today called *Huernia humilis* as it has a very peculiar colouring. Nevertheless, the inner corona lobes appear to be short and the bud is quite flat. This might have convinced N.E. Brown of the identity of this species (Brown 1890) and led to the identification of more recently collected material by him and others as *H. humilis*.

15. *Huernia plowesii*

Huernia plowesii L.C. Leach, *Excelsa Taxon. Ser. 4*: 134 (1988).

Type: Namibia, Tiras Mountains, Plowes 6761 (NBG, holo.; PRE, iso.).

Dwarf succulent forming dense clump up to 300 mm diam. Stems 10-20 (-40) mm long, 8-15 mm thick (excluding teeth), erect, short and stout often somewhat pyramidal, grey-green occasionally marked with purple; tubercles 2-4 mm long, broadly deltoid, spreading, laterally flattened and joined into 4 (-5) angles along stem, tapering to small acute teeth. Inflorescence of 1-5 flowers developing in gradual succession, arising near base of stem from short peduncle (up to 5 mm long) with fine lanceolate bracts $\pm$ 2 mm long without lateral teeth; pedicel 10-18 mm long, 1.5-2.0 mm thick, ascending then spreading usually holding flower facing horizontally (sometimes upwards); sepals 2.5-5.0 mm long, 1.5-2.0 mm broad at base, ovate, acuminate. Corolla 25-40 (-45) mm diam., rotate; outside smooth, cream with 1 heavy (+ 2 fainter) raised longitudinal veins running down centre of each lobe; inside cream coarsely speckled with red or maroon on lobes and more densely blotched with red or maroon on raised slightly shiny annulus to plain red or maroon in tube, on lobes with minute papillae each with shortly acute only slightly swollen maroon-tipped apical bristle, in mouth of tube with stiff fine to slightly clavate dark maroon bristles 1-3 mm long each arising from slightly raised papilla; tube 4-5 mm long, 6-8 mm broad at mouth, cupular, strongly pentagonal, mouth formed by raised annulus (annulus only slightly thickened and forced upwards by strong reflection of mouth below bases of lobes); lobes 8-10 mm long, 15-17 mm broad at base, spreading to reflexed, $\pm$ deltate, acute. Corona $\pm$ 3 mm tall, 2.5-4.0 mm broad, without basal stipe; outer lobes 0.5-1.0 mm long, dark maroon, shortly and obtusely bilobed, spreading to touch base of

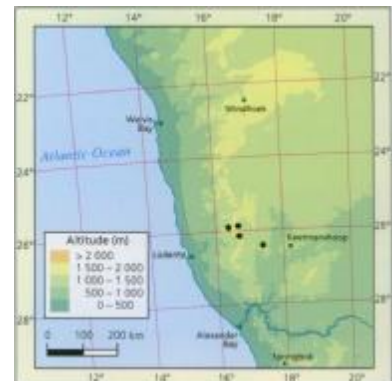


Fig. 5.99. Distribution of *Huernia plowesii*.

tube but not fused to it, inner lobes 0.7-1.0 mm long, maroon to orange, adpressed to backs of anthers, shorter than to exceeding them, tapering from broad transverse dorsal gibbosity to small bristly acute apex.

Distribution and habitat

Huernia plowesii is known from a small area to the west and south of Helmeringhausen in southern Namibia. It seems to be associated mainly with the granite hills of the Tiras Mountains and is of quite wide and general occurrence in them at altitudes of 1 700-1 950 m, that is, mainly in the higher areas. There is also a single record known near Bethanie. Plants are usually rather scattered and they grow on gentle, very stony slopes and plateaux, wedged into crevices between rocks and often under small bushes.



Fig. 5.100. *H. plowesii*, PVB 5731, Tiras Mountains, south-west of Helmeringhausen, Namibia. Here the corolla tube is not so markedly pentagonal.

Diagnostic features and relationships

Specimens of *H. plowesii* form often quite large clumps which may reach 300 mm in diameter. Large specimens consist of enormous numbers of extremely tightly packed and often very small stems. In this species the stems are a little smaller than in *H. humilis* and often seem to have slightly more sharply pointed tubercles.

In *H. plowesii*, the buds, from being bell-shaped when small, become quite remarkably flat before opening and may be up to 20 mm broad and only 5 mm long.

The flowers of *H. plowesii* are mottled inside with irregular, very bold to quite inconspicuous

red or maroon spots on a cream background on the lobes and on the base on the annulus. This changes to larger spots on the annulus and then sometimes coalesces there to shiny red or maroon. The tube is uniformly red or maroon and quite shiny at the base. The annulus is even more pronounced than in *H. humilis* and is up to four times as thick as the rest of the corolla tube but its prominence is still at least partly caused by the reflexion of the corolla just below the lobes. The apical bristles on the small papillae found on the lobes are rather more variable in thickness in *H. plowesii* than in *H. humilis* and they may be quite slender (in which case they approach those found in *H. zebrina*) to relatively stout. There may be relatively few



Fig. 5.101. *H. plowesii*, PVB 5705, Barbi, west of Helmeringhausen, Namibia, with a markedly pentagonal tube.

(sometimes as little as 10 or fewer) of the larger bristles around the mouth of the corolla tube.

The dark maroon corona is scarcely visible against the colour of the corolla tube. The outer lobes are extremely variable in length, from short as in *H. humilis* to spreading widely on the base of the tube. The inner lobes often ascend somewhat above the anthers.

History

This very beautifully flowered *Huernia* was discovered by Ernst F.T. Rusch sometime before 1937 on the farm Barbi, which lies to the west of Helmeringhausen. A photograph that he had taken of a flower was printed in White & Sloane (1937: fig. 965-A). They placed this tentatively under *H. guttata* and this identification was repeated by Huber (1967) in his account of *Huernia* in the *Prodromus einer Flora von Südwestafrika*. It appears to have been recollected for the first time by H.A.G. Hansen in 1975, again near Helmeringhausen, but it remains known from only a few collections.



Fig. 5.102. *H. plowesii*, PVB 8093, western end of the Tiras Mountains, Namibia.

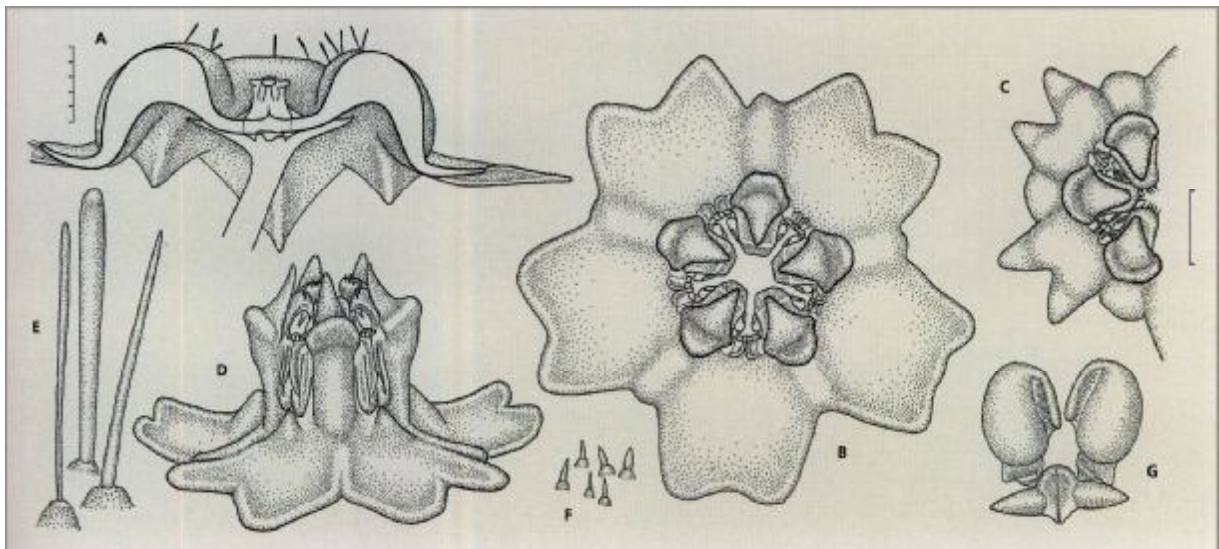


Fig. 5.103. *Huernia plowesii*. A, side view of dissected flower. B, C, face view of gynostegium (or part of it). D, side view of gynostegium. E, papillae inside corolla on annulus. F, papillae inside corolla on lobes. G, pollinarium. Scale bars: A, 5 mm; B-D, 1 mm (at C); E, F, 0.5 mm (at C); G, 0.25 mm (at C). Drawn from A, E, F, PVB 5705, Barbi, west of Helmeringhausen, Namibia; B, D, G, PVB 3152, Tiras, Namibia; C, Kratz, Helmeringhausen, Namibia.

HUERNIA ZEBRINA

16. *Huernia zebrina*

Huernia zebrina N.E.Br., Fl. Cap. 4 (1): 921 (1909).
Type: South Africa, Natal, Eshowe, Saunders (K).

Small succulent forming dense to diffuse clump to 0.5 m diam. Stems 15-20 mm long, 8-20 mm thick (excluding teeth), erect to decumbent, grey-green usually mottled with purple; tubercles 4-7 mm long, deltoid, laterally flattened and joined into 4-5 (-6) angles along stem, narrowing abruptly into slender tooth. Inflorescence of 1-3 flowers developing in gradual succession, arising from short peduncle (up to 5 mm long) with filiform bracts 3-4 mm long; pedicel 15-20 mm long, 2 mm thick, ascending then spreading to hold flower facing horizontally; sepals 8-10 mm long, 2 mm broad at base, ovate, acuminate. Corolla (25-) 35-45 (-50) mm diam., rotate, glabrous; outside cream often mottled with reddish behind annulus and on lobes with 1 heavy (+ 2 fainter) raised longitudinal veins running down centre of each lobe; inside cream transversely and irregularly lined with red to maroon on lobes changing to ± circular dots on shiny annulus often coalescing there and uniformly red to maroon in tube, with minute fine spike-like papillae on lobes but otherwise ± free of bristles and papillae (especially in tube); tube 6-7 mm long, 6-8 mm broad at mouth, cupular, cylindrical, mouth formed by raised annulus (annulus only slightly thickened and forced upwards by strong reflexion of corolla below bases of lobes); lobes 10-15 mm long, 15-20 mm broad at base, spreading, deltate, shortly acuminate. Corona 3.5-4.0 mm tall, 5.0-6.5 mm broad, without basal stipe; outer lobes 1.5-2.0 mm long, deeply to shallowly bilobed into obtuse to truncate lobules, spreading to touch base

of tube but not fused to it, cream with red to maroon margins; inner lobes 0.7-1.0 mm long, red to maroon with bright yellow dorsal gibbosity, adpressed to backs of anthers, shorter than to slightly exceeding them and not meeting at centre, tapering from broad transverse dorsal gibbosity to narrowly obtuse smooth apex.

Huernia zebrina shares with both *H. humilis* and *H. plowesii* the conspicuous annulus and the short inner corona lobes. The three species differ most obviously in that the corolla lobes are spotted inside in *H. humilis* and *H. plowesii* and are transversely striped in *H. zebrina*. *H. zebrina* entirely lacks the larger bristles found around the mouth of the tube in *H. plowesii* (and rarely in *H. humilis*). In all three species the lobes are covered with fine papillae which are only just visible to the naked eye. In *H. zebrina* these papillae have an attenuated apical cell whereas in *H. humilis* and *H. plowesii* the apical cell of each is swollen and acute.

Leach (1988) separated *H. insigniflora* from *H. zebrina* by the erect, more clump-forming habit, the stouter almost square stems with smaller teeth and the grey-green colour. He also found that in *H. insigniflora* the flowers were

'more variable in colour...[with] the lobes... sometimes irregularly marked with...more or less transverse blotches, quite different from the distinct "zebra" stripes of *H. zebrina*' and that the corona was cream in both but had a dark margin in *H. zebrina*. He also mentioned their 'quite different habitats'.

My own collecting has shown that flowers of *H. insigniflora* are quite extraordinarily variable in colour. The annulus always seems to be shiny red (sometimes quite dark) and it is the colour of the lobes that is most changeable. Some flowers have brilliant transverse bars of pale to dark red on the lobes and these may even continue onto the edges of the annulus (fig. 5.118). Others are only rather faintly barred and still others have no bars at all, in which case the lobes are plain cream. The fine papillae on the lobes are usually reddish and give the lobes in such cases a faint, reddish hue. It seems that plants with cream corolla lobes have been assumed to represent '*insigniflora*' but the existence of forms where the colour of the corolla is indistinguishable from that in *H. zebrina* has not generally been acknowledged. In fact it appears that most populations of

Key to the subspecies of *H. zebrina*

- Stems at least 30 mm long, 5-(-6-) angled, annulus shiny 16a. subsp. *zebrina*
Stems usually < 30 mm long, 4-angled, annulus not shiny 16b. subsp. *insigniflora*

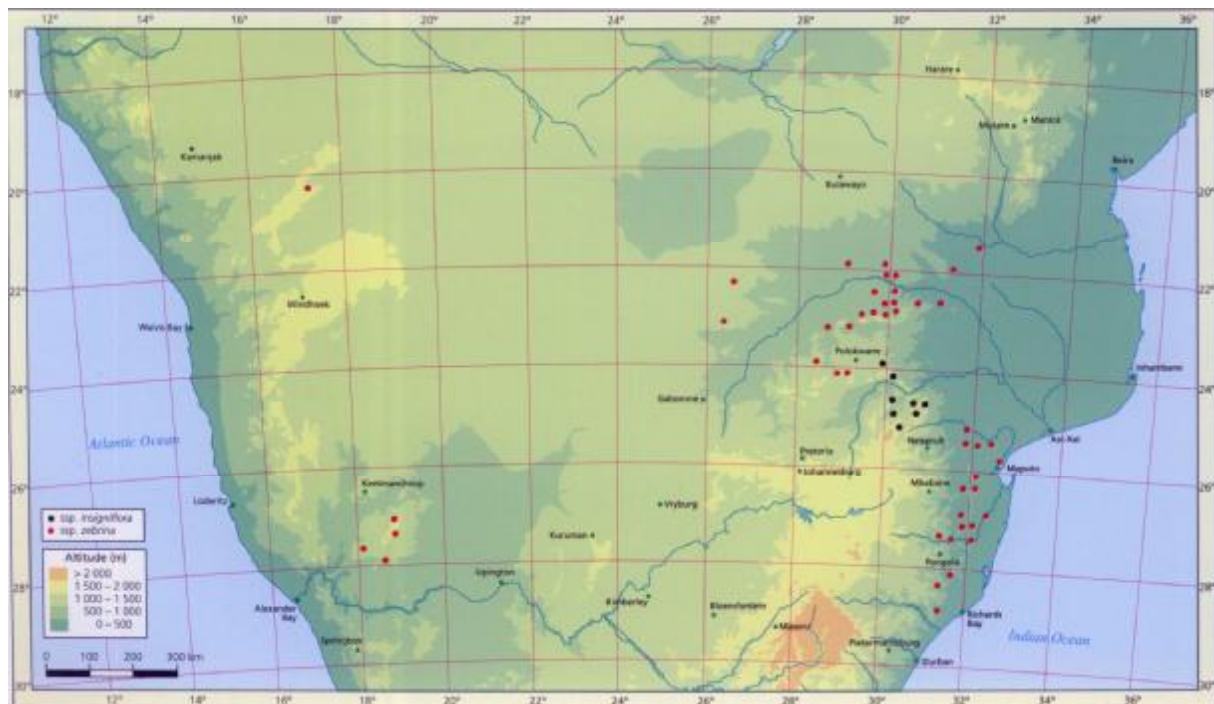


Fig. 5.104. Distribution of *Huernia zebrina*.



Fig. 5.105. *H. zebrina* subsp. *zebrina*, PVB 6556, Ga-Mankodi, south of Blouberg, in habitat, January 1996.

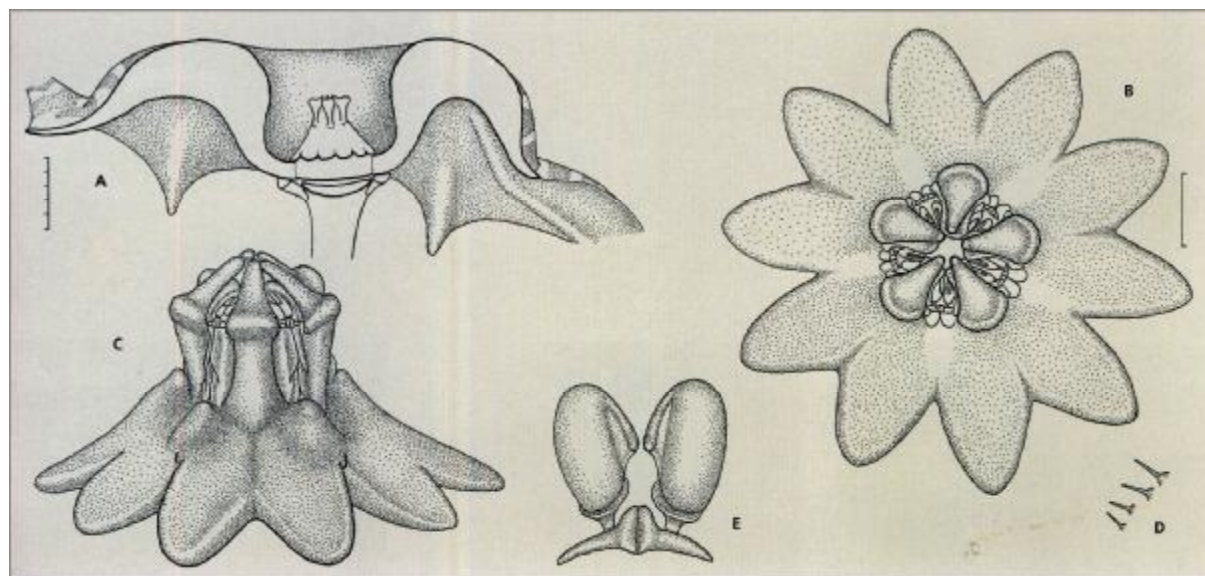


Fig. 5.106. *Huernia zebrina* subsp. *zebrina*. A, side view of dissected flower. B, face view of gynostegium. C, side view of gynostegium. D, papillae inside corolla on lobes. E, pollinarium. Scale bars: A, 5 mm; B, C, 1 mm (at B); D, 0.5 mm (at B); E, 0.25 mm (at B). Drawn from A, PVB 6429, south of Shoshong, Botswana; B-E, PVB 3533, eastern side of the Great Karas Mountains, Namibia.

HUERNIA ZEBRINA

'*insigniflora*' contain a broad mixture of colour variants ranging from '*insigniflora*' to '*zebrina*'. The same fine, acuminate papillae that are typical of *H. zebrina* are present on the lobes in *H. insigniflora*. The outer corona in '*insigniflora*' is cream to faintly reddish, sometimes with a reddish margin.

In respect of the 'erect, more clump-forming habit, the stouter almost square stems with smaller teeth' it should be noted that it has often been found that plants growing on exposed rock surfaces (at whatever altitude) tend to have a more compact growth with shorter and thicker stems than those growing in low-lying areas away from exposed rock surfaces (and the same variation has been found, for example, between *H. hislopiae* subsp. *hislopiae* and subsp. *robusta*). Consequently, this distinction between *H. zebrina* and *H. insigniflora* is almost certainly linked to the different ecological circumstances under which they occur. I can find no reason, therefore, to maintain these as distinct species and *H. zebrina* is treated here as having two subspecies.



Fig. 5.107. *H. zebrina* subsp. *zebrina*, PVB 4441, Ulundi.



Fig. 5.108. *H. zebrina* subsp. *zebrina*, PVB 4447, near Ulundi.



Fig. 5.109. *H. zebrina* subsp. *zebrina*, PVB 6556, Gankodi, south of Blouberg, in habitat, January 1996.

16a. *Huernia zebrina* subsp. *zebrina*

Huernia blackbeardiae R.A.Dyer ex Jacobsen, *Die Sukkulente*: 75 (1933).

Type: Botswana, Serowe, *Blackbeard* (GRA, holo.; PRE, iso.).

Huernia zebrina var. *magniflora* E.Phillips, *Fl. Pl. South Africa* 16: t. 613 (1936).

Huernia zebrina subsp. *magniflora* (E.Phillips) L.C. Leach, *Excelsa Taxon. Ser.* 4:139 (1988).

Type: Transvaal, Potgietersrus, *Ralston* sub PRE 20568 (PRE).

Stems decumbent, 30-120 mm long; *tubercles* 5-7 mm long, joined into 5 (-6) angles along stem. *Corolla* (25-) 35-50 mm diam.; inside cream and very brightly transversely striped with red to maroon on lobes changing to $\pm$ circular dots on edge of shiny annulus.

Distribution and habitat

Subsp. *zebrina* is widely and very patchily distributed across southern Africa. On the eastern side of the subcontinent it is quite common in Limpopo Province, mainly in the somewhat lower-lying basin of the Limpopo River. In Zimbabwe it is found in the south only, also mainly along the valley of the Limpopo. Records have also been made in Swaziland, southern Mozambique and in KwaZulu-Natal as far south as Eshowe. Towards the west the distribution becomes far more disjointed and it occurs in an area around Serowe in Botswana and in two widely separated areas in Namibia. One of these is around the base of the Great Karas Mountains in the south and the other is near the foot of the Waterberg in the north.

Plants grow in stony areas, often with calcareous or hard loam among bushes and small trees.

Diagnostic features and relationships

Specimens of subsp. *zebrina* may reach a considerable size and plants 300 mm across are not unusual, but they are fairly loosely

clump-forming. The stems are usually fairly robust, with five wings along them formed by the tubercles.

Subsp. *zebrina* has probably the most gorgeous flowers amongst all the southern African stapeliads. They are often large and at 35-50 mm across are amongst the broadest in the genus. This is also the most impressive of the 'lifebuoy Huernias', with a thick, shiny ring around the mouth of the tube. The lobes are fairly strongly reflexed around the mouth of the tube but this ring is mainly formed by a thickening of the corolla which reaches a maximum of about three times its normal thickness in the annulus. The tube and much of the annulus are uniformly red to maroon. Towards its outer edge the annulus becomes broadly spotted with maroon on cream and this changes to transverse maroon bars on a cream background on the lobes. In this species the centre of the flower is smooth, as is indicated by its shininess, but the lobes are not shiny at all and their surface is covered with small papillae, each of which is tipped by a fine, attenuated, spindle-shaped bristle.

As in many species, the outer corona is very variable in length, sometimes spreading out on the base of the tube. It is usually cream with red or maroon margins but may be almost wholly maroon. The inner corona lobes are short, though just slightly longer than the anthers, and are bright yellow with red or maroon edges.

History

Not much is known about how subsp. *zebrina* came to be discovered but specimens were sent to N.E. Brown by Katherine Saunders of Tongaat Sugar Estates. She had, in turn, obtained them from the wife of her son, Charles J.R. Saunders, a one-time magistrate who was resident for a time in Eshowe. The plants seem to have been collected near Eshowe, probably before 1900.



Fig. 5.110. *H. zebrina* subsp. *zebrina*, PVB 3533, eastern side of the Great Karas Mountains, Namibia.



Fig. 5.111. *H. zebrina* subsp. *zebrina*, PVB 3533, eastern side of the Great Karas Mountains, Namibia.

16b. *Huernia zebrina* subsp. *insigniflora*

Huernia zebrina subsp. *insigniflora* (C.A.Maass)
Bruyns, comb. et stat. nov.

Huernia insigniflora C.A.Maass, Möllers Deutsche
Gärtn.-Zeitung 43: 79 (1928).

Neotype: South Africa, Transvaal, Pretoria distr.,
Maass (K).

Huernia confusa E.Phillips, Fl. Pl. South Africa 12: t.
456 (1932).

Type: near Haenertsburg, Schweickerdt sub PRE
1299 (PRE).

Stems erect, 15-30 (-40) mm long; *tubercles* 4-5 mm long, joined into 4 (-5) angles along stem. *Corolla* 25-35 mm diam; inside uniformly cream to rose, often faintly (rarely more brightly) transversely striped with red to maroon on lobes changing to $\pm$ circular dots on edge of annulus.

Distribution and habitat

Subsp. *insigniflora* is found along the northern parts of the Drakensberg from Tzaneen to Pilgrim's Rest, mainly at altitudes of between 1200 and 1700 m.

Specimens have been recorded on granite slopes around Tzaneen, on dolomite outcrops further south from The Downs to the Blyde

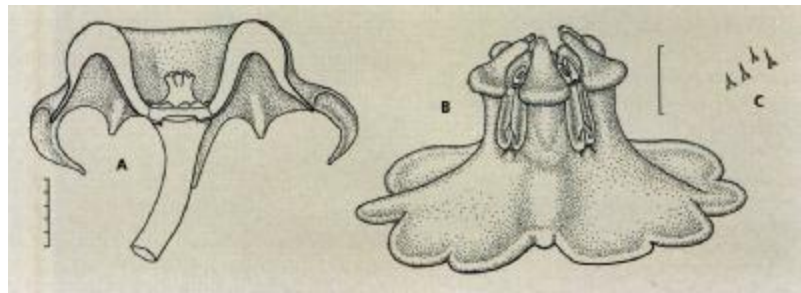


Fig. 5.112. *Huernia zebrina* subsp. *insigniflora*. A, side view of dissected flower. B, side view of gynostegium. C, papillae inside corolla on lobes. Scale bars: A, 5 mm; B, 1 mm; C, 0.5 mm (at B). Drawn from A, PVB 6608, Ohrigstad Dam; B, C, PVB 6620, Maope, Steelpoort.

River Canyon, and on dolerite slabs near Steelpoort so it appears to be very unparticular about the type of soil in which it grows. In these situations it is usually found on mountain slopes on bare patches of exposed rocks or among bushes along the edges of such exposed slabs.

Diagnostic features and relationships

Plants of subsp. *insigniflora* form dense, tightly packed clumps of relatively short, 4-angled stems.



Fig. 5.113. *H. zebrina* subsp. *insigniflora*, PVB 6620, Maope, Steelpoort, with more or less unmarked flowers, as was supposed to be typical of *H. insigniflora*.



Fig. 5.114. *H. zebrina* subsp. *insigniflora*, PVB 7023, near Blyde River Canyon, growing in crevices in dolomite outcrop with a form of *Euphorbia schinzii* and other small succulents, January 1997.

HUERNIA BARBATA

The flowers are much more variable in colour on the lobes than those of subsp. *zebrina*. The original material that Maass obtained had plain 'rose' lobes without markings and a dark purple-brown annulus. The plants described by E.P. Phillips as *Huernia confusa* had irregular light red markings on a paler background on the lobes and again a dark annulus. At localities where several plants have been collected, it has been found that almost every possible variant between these occur and that even darker stripes than those described for *H. confusa* may exist on the lobes.

In subsp. *insigniflora* the outer corona lobes are usually cream suffused slightly with pink and they spread broadly on the base of the tube. The inner lobes are exactly as in subsp. *zebrina*, that is, bright yellow with maroon margins. Whereas the outer lobes blend in closely with the colour of the tube, the inner lobes are comparatively conspicuous.

History

As discussed by White & Sloane (1937) and Leach (1988), the origin of the material that C.A. Maass described remains unclear, though



Fig. 5.115. *H. zebrina* subsp. *insigniflora*, PVB 6620, Maope, near Steelpoort, with yet more faintly marked flowers.

it seems likely that it was collected by the entomologist and stapeliad enthusiast Georges van Son around 1927. The material later described as *Huernia confusa* was first observed by Rudolf Schlechter in April 1894 and he considered that this material represented *H. humilis*, though N.E. Brown (1907-09) had already expressed doubt about this. It was recollected just before 1932 by Schweickerdt at more or less the same spot where Schlechter had found it and this gathering was given the name *H. confusa*.



Fig. 5.116. *H. zebrina* subsp. *insigniflora*, PVB 6598, near The Downs, near Tzaneen.



Fig. 5.117. *H. zebrina* subsp. *insigniflora*, PVB 6620, Maope, near Steelpoort, with somewhat more faintly marked flowers.



Fig. 5.118. *H. zebrina* subsp. *insigniflora*, PVB 6598, near The Downs, near Tzaneen, with flowers very similarly coloured to those of subsp. *zebrina*.

17. *Huernia barbata*

Huernia barbata (Masson) Haw., Syn. PL Succ.: 31 (1812).

Stapelia barbata Masson, Stap. Nov.: 11, t. 7 (1796).

Type: South Africa, Masson (missing).

Lectotype: Masson, Stap. Nov.: t. 7.

Dwarf succulent forming dense clump up to 300 mm diam. Stems 10-60 (-100) mm long, 6-20 mm thick, shortly decumbent, often very stout, grey-green sometimes mottled with purple-red; tubercles 4-6 mm long, deltoid, spreading, laterally flattened and joined into 4-5 angles along stem. Inflorescence of 1-5 flowers developing in gradual succession, arising near base of stem on short peduncle (up to 5 mm long) with fine lanceolate bracts 2-3 mm long; pedicel 4-12 mm long, 1.5 mm thick, ascending to spreading with ascending apex, holding flower facing upwards or outwards; sepals 3-8 mm long, 1.0-1.5 mm broad at base, attenuate. Corolla 15-65 mm long, 14-60 mm diam., tubular-campanulate to bicampanulate; outside smooth, creamy to greenish sometimes speckled with maroon, with 3-5 raised longitudinal veins running from lobes to base of tube; inside cream to pale yellow with rounded maroon spots becoming larger towards mouth of tube and changing to narrow concentric broken lines or plain maroon in lower half of tube, covered except in lower third of tube (sometimes only around mouth of tube) with minute maroon spherical-tipped papillae (densely crowded towards margins of lobes) interspersed with larger obtuse conical papillae each tipped by clavate bristle 1-3 mm long (longest in mouth of tube becoming shorter on lobes and disappearing around middle of lobes); tube 5-20 mm long, 10-12 mm broad at mouth, widening towards mouth from cupular base, cylindrical, often with corolla somewhat thickened towards mouth; lobes 3-18 mm long, 6-17 mm broad at base, ascending to recurved, narrowly deltate and usually longer than wide, acuminate to attenuate. Corona 7-9 mm tall, 5-8 mm broad, without basal stipe; outer lobes spreading on base of tube and mostly fused to it, fused together into disc with crenulate with raised margin (forming shallow plate around gynostegium) to 5-lobed with each lobe deeply bifid, deep maroon; inner lobes 3-5 mm long, deep maroon to cream or pink and mottled with brown, adpressed to backs of anthers near their base, rising above their apices and connivent then diverging, dorsiventrally flattened around laterally broadened base becoming terete above and tapering gradually to fine apex.

Leach (1988) separated the three 'species' *H. barbata*, *H. campanulata* and *H. clavigera* on a labyrinthine maze of minor characters. In *H. barbata* the exterior of the corolla is minutely speckled or immaculate; inside the corolla is concentrically lined in the tube and bristles are found in the throat of the tube, extending onto the limb and lobes. In *H. campanulata* the outside of the corolla is sparingly red-blotched; inside the tube is 'irregularly ± concentrically dark camine lined in the tube, the lines usually merging into solid colour in the lower part of the tube' (p. 13) and bristles are found at the mouth of the tube only. In *H. clavigera*

the outside is variably minutely speckled or immaculate; inside the tube is 'solid blackish maroon in the lower portion' (p. 13) and the clavate bristles in the tube extend to the bases of the lobes.

There seems to be no point in recognising all these species, particularly as the extent of variation within each (especially *H. clavigera*) is enormous and Leach admitted (p. 26) that *H. clavigera* 'occasionally displays odd characters of both [of the other] species'. So, for example, he found specimens of *H. clavigera* where the bristles inside the corolla are restricted to the mouth of the tube as in *H. campanulata*. However, he dismissed this with the remark that 'such convergencies are of very scattered occurrence and show no signs of being clinal in origin', thereby avoiding the issue of whether these two 'species' were really distinct.

In the case of *H. barbata* (p. 31) he gave the 'tubular-campanulate, not at all bicampanulate' flower as the most important character, separating it from the others. However, in '*H. ingeae*' (which he included under *H. clavigera*) the corolla is also campanulate and, indeed, in the description of *H. clavigera* he mentioned the existence of 'campanulate flowers from 18-20 mm long' (p. 25) too, so this character actually cannot be used to separate them reliably. He admitted too (p. 31) that 'all other characters are so variable that it is extremely difficult to find reliable key characters'. The situation suggests clearly that a reduction in the number of species is necessary.

One appears then to be dealing with a single species. *Huernia barbata* is widely distributed from the Eastern Cape to near the Orange River in Bushmanland. It is also found

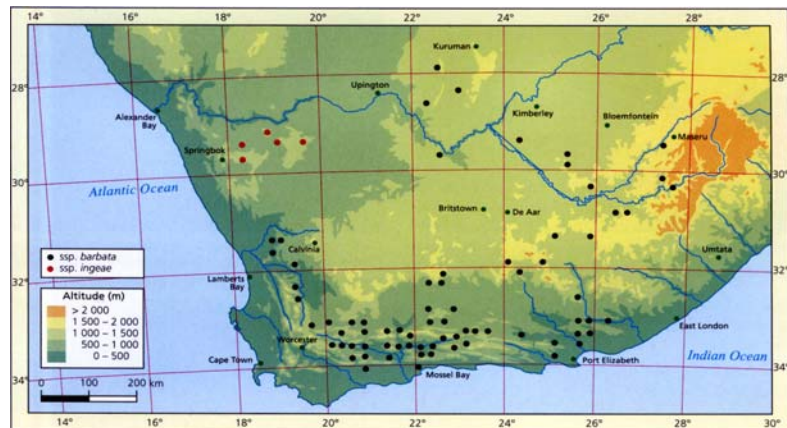


Fig. 5.119. Distribution of *Huernia barbata*.

Key to the subspecies of <i>H. barbata</i>	
Stems mostly < 20 mm long and < 10 mm thick, corolla 15–20 mm long, corolla lobes 3–6 mm long	17b. subsp. ingeae
Stems generally more than 20 mm long and 10 mm thick, corolla 25–65 mm long, corolla lobes 9–18 mm long	17a. subsp. barbata



Fig. 5.120. *H. barbata* subsp. *barbata*, PVB 3061, south-east of Laingsburg on road to Seweweekspoort. In this population the fine spotting of the corolla and its shape are very suggestive of *H. longituba*.

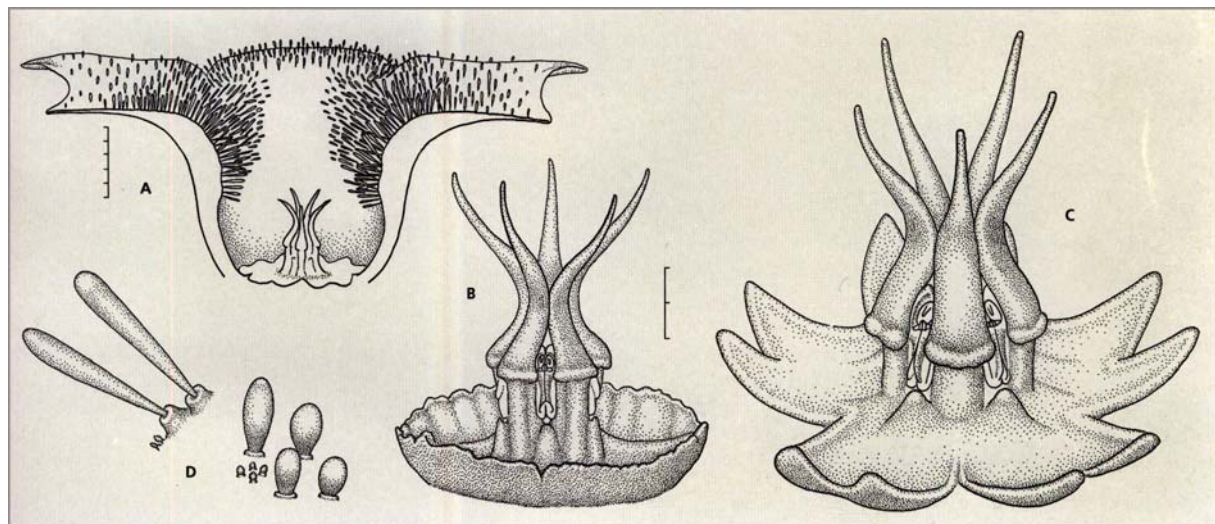


Fig. 5.121. *Huernia barbata* (A, B, D, subsp. *barbata*, C, subsp. *ingeae*). A, side view of dissected flower. B, C, side view of gynostegium. D, papillae inside corolla: long ones from around mouth of tube, broad, short ones on lobes. Scale bars: A, 5 mm; B, 2 mm; C, D, 1 mm (at B). Drawn from A, PVB 7810, Nougaspoort (no specimen); B, D, PVB 4221, slightly west of Beaufort West; C, PVB 2534, Pofadder.

17a. *Huernia barbata* subsp. *barbata*

Stapelia campanulata Masson, *Stap. Nov.*: 11, t. 6 (1796).

Huernia campanulata (Masson) Haw., *Syn. Pl. Succ.*: 28 (1812).

Type: South Africa, Masson (missing).

Lectotype: Masson, *Stap. Nov.*: t. 6.

Stapelia clavigera Jacq., *Stap.*: t. 5 (1806-19).

Huernia clavigera (Jacq.) Haw., *Suppl. Pl. Succ.*: 10 (1819).

Lectotype: Jacq., *Stap.*: t. 5.

Stapelia tubata Jacq., *Stap.*: t. 3 (1806-19).

Huernia tubata (Jacq.) Haw., *Syn. Pl. Succ.*: 30 (1812).

Huernia barbata var. *tubata* (Jacq.) N.E.Br. *Fl. Cap.* 4 (1): 907 (1909).

Lectotype: Jacq., *Stap.*: t. 3.

Stapelia duodecimfida Jacq., *Stap.*: t. 4 (1806-19).

Huernia duodecimfida (Jacq.) Sweet, *Hort. Brit.* ed. 2: 359 (1830).

Huernia tubata var. *duodecimfida* (Jacq.) G. Don, *Gen. Syst.* 4: 113 (1838).

Lectotype: Jacq., *Stap.*: t. 4.

Huernia barbata var. *griqualensis* N.E.Br., *Fl. Cap.* 4 (1): 907 (1909).

Type: South Africa, Cape, Griqualand West, *Tuck sub MacDwan* 2245 (K, holo.; PRE, SAM, iso.).

Huernia campanulata var. *denticoronata* N.E.Br., *Fl. Cap.* 4 (1): 906 (1909).

Type: near Laingsburg, N.S. *Pillans* 157 (BOL).

Huernia clavigera var. *maritima* N.E.Br., *Fl. Cap.* 4 (1): 908 (1909).

Type: Mossel Bay, N.S. *Pillans* 703 (BOL).

Huernia decemdentata N.E.Br., *Fl. Cap.* 4 (1): 908 (1909).

Type: South Africa, *Rabjohn* (K).

Stems 20-60 mm long, 10-20 mm thick, 4-5-angled.

Corolla 25-65 mm long, 15-60 mm diam., campanulate to bicampanulate; inside with larger obtuse conical papillae each tipped by clavate bristle 2-3 mm; **tube** 10-20 mm long, generally widening towards mouth; **lobes** 9-18 mm long, 15-17 mm broad at base.

Distribution and habitat

In the Western Cape subsp. *barbata* is found around Vanrhyn's Pass through the eastern, dry parts of the Cedarberg to the Little Karoo and from here it continues eastwards to Grahams-town. It also occurs very sporadically in the Great Karoo, from Fraserburg to Beaufort West and then on the eastern edge to Middleburg. There are a few, widely scattered records in the eastern parts of the Northern Cape (in what

was previously known as Griqualand West) and from the eastern parts of the Free State. In Lesotho it has been recorded in the west and in the south-western corner of the country.

Generally plants are found on stony slopes amongst rocks and under small bushes, often filling spaces between rocks with tightly packed clusters of stems.

Diagnostic features and relationships

The stems of subsp. *barbata* are mostly 4-angled and quite robust. Stems with 5 angles are especially prevalent in the area from the Cedarberg to Vanrhyn's Pass. When exposed to the sun they are generally much shorter and are more densely mottled with purple than those which are sheltered, where they may be up to 100 mm long.

Some very magnificent-flowered forms of subsp. *barbata* exist in which the flowers are up to 60 mm across and where the fairly broad but deep tube is up to 20 mm long with the lobes spreading from its mouth. Flowers of both subspecies are campanulate, with a cylindrical tube around the corona, usually at least as long as broad. The shape of the flower around the mouth of the tube is particularly variable. In



Fig. 5.122. *H. barbata* subsp. *barbata*, PVB 5392, east of Murraysburg, in habitat among dolerite rocks and short grasses, January 1993.

many cases there is a flat, united area around the mouth (sometimes referred to as the 'limb' of the corolla) and then the lobes may spread out to extend this flat area or may be erect around it. In the latter case the flower forms a broad, shallow 'secondary' tube beyond the central one (e.g. fig. 5.125) and is then usually referred to as 'bicanpanulate'. However, in some cases the flat area is entirely absent, with the corolla tube merely experiencing a slight broadening close to the bases of the lobes and the lobes erect around its mouth (and continuing the tube) or spreading. The sinuses of the lobes usually form fairly conspicuous intermediate lobules between adjacent lobes, which can be up to 5 mm long.

In subsp. *barbata* the flower rarely has a bold colouring inside and it is invariably finely spotted with roundish maroon spots on a cream background. Inside the tube these spots gradually become longer to form concentric rings of maroon in the lower half or it is wholly maroon there. The corolla is usually thickened around the middle of the tube, though this is only obvious if it is dissected. Around the level of this thickening, the surface becomes adorned with papillae and, in one form or another, these papillae continue from here to the tips of the lobes but are entirely absent below this level. These papillae consist of a low, thickened base (fig. 28 C, D) which bears an enormously enlarged, clavate apical cell up to 3 mm long. The upper part of each papilla and the apical cell are usually maroon. The apical cells gradually become smaller and fewer on the lobes. Over most of the surface they are interspersed with minute versions of the same things which are a tiny fraction of the size of the large ones but have the same structure: a multicellular, conical base with a single, swollen, dark apical cell. These small papillae become particularly numerous towards the edges and tips of the lobes and, where they are densely encrusted, the flower has a dark, velvety tinge (fig. 5.125).

In general the outer corona is dark maroon. The lobes are often fused into a shallowly plate-like or indistinctly 5- or 10-angled disc but also may be rectangular and bifid towards the apices. They spread out on the base of the tube and are partly fused to it. The inner lobes are often paler maroon than the outer coronal disc and taper to fine, slender points. They are often covered with fine, sweat-like drops of what might be nectar.

History

Subsp. *barbata* was discovered by Francis Masson and he gave names to two of his collections of it, namely *Stapelia barbata* and *S. campanulata*. *Stapelia barbata* flowered in his garden in Cape Town in March 1794 but he gave no intimation as to where either this or *S. campanulata* had been collected.



Fig. 5.123. *H. barbata* subsp. *barbata*, PVB 6172, Kobee Pass, south-east of Vanrhynsdorp. In this area the flowers have a particularly broad, flat 'limb' outside the tube.



Fig. 5.124. *H. barbata* subsp. *barbata*, PVB 5013, Dikkop flats, north of Grahamstown.



Fig. 5.125. *H. barbata* subsp. *barbata*, PVB 3686, Tierberg, Prince Albert.



Fig. 5.126. *H. barbata* subsp. *barbata*, PVB 4221, slightly west of Beaufort West, plants with especially large flowers.

In Lesotho it was first noted in the Quthing district by A. Dieterlin in 1913, though this seems to have been missed by Phillips (1917), where '*Stapelia flavirostris*' is the only stapeliad

recorded from Lesotho. Amy Jacot Guillarmod (1971) found it again near Maseru and also in the south-west during her exploration of the country.

17b. *Huernia barbata* subsp. *ingeae*

Huernia barbata subsp. *ingeae* (Lavranos)

Bruyns, *comb. et stat. nov.*

Huernia ingeae Lavranos, *Cact. & Succ. J. (US)* 54: 99 (1982).

Type: South Africa, Cape, Namies, *Pehlemann sub Lavranos 17573* (NBG).

Stems 10-20 (-40) mm long, 6-10 (-12) mm thick, (4-) 5-angled. **Corolla** 15-20 mm long, 14-16 mm diam., campanulate to rarely bicanpanulate; inside with larger obtuse conical papillae each tipped by clavate bristle 2-3 mm; **tube** 10-20 mm long, generally widening towards mouth; **lobes** 3-6 mm long, 6-9 mm broad at base.

Distribution and habitat

This subspecies is found exclusively in the arid and rocky hills of Bushmanland from a little north-east of Springbok to around Pofadder. It is only known from the south bank of the Orange River.

Plants are found on white, quartz hills which rise some 50-300 m above the surrounding plains. Many of these hills support a very high concentration of dwarf and often extremely localised succulents, particularly



Fig. 5.127. *H. barbata* subsp. *ingeae*, PVB 5245, north-west of Pofadder, Bushmanland.



Fig. 5.128. *H. barbata* subsp. *ingeae*, PVB 4660, Naip se Berg, Bushmanland.

belonging to the succulent Aizoaceae and the Crassulaceae. Specimens of this stapeliad usually grow tightly wedged in sheltered crevices between lumps of quartz, usually on the summit of these hills.

Diagnostic features and relationships

Subsp. *ingeae* is remarkable for its extremely tiny, almost always 5-angled stems that form dense, tightly packed clumps. The stems are mostly not more than 20 mm long and 10 mm thick. In their small size, they resemble those of *H. hallii* and *H. plowesii* quite closely.

The flowers of subsp. *ingeae* are always small and mostly reach a maximum length of about 20 mm. They are mostly campanulate rather than bicanpanulate and the relatively short lobes are more or less erect around the mouth of the tube. Internally the flower does not differ significantly from other forms of *H. barbata*, being covered with similar papillae with a small thickened base and a massively enlarged, club-shaped apical cell. The outer corona always seems to consist of five apically bifid lobes and disc-like outer coronas such as occur periodically in subsp. *barbata* have not been seen here. The inner corona consists of slender, connivent and then spreading and acuminate lobes as is usual for the species.

History

Subsp. *ingeae* was first recorded by Herklaas A. Horn, who was at one time the Town Clerk of Koffiefontein in the Free State and collected succulents commercially on a small scale. He found it at Namies in December 1961. It was described (as *Huernia ingeae*) from plants collected at Namies by Inge Pehlemann, but Leach (1988) did not recognise it at all.

18. *Huernia piersii*

Huernia piersii N.E.Br., *F. Cap.* 4 (1): 909 (1909).

Type: South Africa, Eastern Cape, near Sterkstroom, Piers sub *N.S. Pillans 622* (K, holo.; BDL, iso.).

Dwarf succulent forming dense clump up to 200 mm diam. **Stems** 10-30 (-50) mm long, 10-20 mm thick, very shortly decumbent, short and stout, grey-green sometimes mottled with purple-red; **tubercles** 3-5 mm long, deltoid, spreading, laterally flattened and joined into 4 (-5) angles along stem. **Inflorescence** of 1-5 flowers developing in gradual succession, arising near base of stem on short peduncle (up to 5 mm long) with fine lanceolate bracts 2-3 mm long; **pedicel** 4-12 mm long, 1.5 mm thick, ascending to spreading with ascending apex, holding flower facing upwards or outwards; **sepals** 3-4 mm long, $\pm$ 1.5 mm broad at base, attenuate. **Corolla** 25-40 mm diam., rotate with short tube in centre; outside smooth, cream to greenish sometimes speckled with maroon, with 3-5 raised longitudinal veins running from lobes to base of tube; inside cream to pale greenish yellow with rounded red-brown to maroon spots becoming larger and coalescing transversely towards mouth of tube and changing to narrow concentric broken red-brown to maroon lines in tube with solid red-brown to maroon patch around corona, covered (mainly on lobes) with minute cream to maroon swollen-acute-tipped papillae changing near bases of lobes to larger obtuse conical papillae ($\pm$ 0.5 mm long) each tipped by slightly clavate bristle 1-2 mm long and continuing to just below mouth of tube; **tube** 5-6 mm long, 6-8 (-12) mm broad at mouth, often slightly constricted at mouth, cupular, with corolla very slightly thickened towards mouth; **lobes** 7-12 mm long, 9-11 mm broad at base, spreading to recurved, narrowly deltate, acuminate. **Corona** $\pm$ 5 mm tall, $\pm$ 5 mm broad, without basal stipe; **outer lobes** spreading on base of tube and mostly fused to it, 5-lobed with each lobe bifid near apex, deep maroon; **inner lobes** $\pm$ 3 mm long, maroon to reddish, adpressed to backs of anthers near their base, rising above their apices and connivent then diverging slightly, dorsiventrally flattened around laterally broadened base becoming terete above and tapering gradually to fine apex.

Leach (1988) included an odd assemblage of collections under *H. piersii*, among which was one from near Graaff-Reinet (PVB 1763), another from Aberdeen and two from near Steytlerville. The collection from near Graaff-Reinet may be a hybrid between *H. barbata* and *H. thuretii*, but is included here under *H. piersii*. Those from near Steytlerville are forms of *H. thuretii* with rather longer bristles on the papillae than usual. Here the concept of *H. piersii* is restricted to material from Graaff-Reinet to the type locality near Sterkstroom and from similar habitats further north-west of Sterkstroom.

Distribution and habitat

Near Sterkstroom this species grows together with *Duvalia caespitosa* and *Stapelia grandiflora* and there are fair numbers of plants of *H. piersii*, forming small mats among stones on a

very unusual series of otherwise almost bare domes of dolerite which constitute the northern slopes of the Andriesberg. This locality harbours a number of other unusual succulents, including *Brachystelma circinatum*, *Ceropegia bowkeri*, the recently described *Neohenricia spiculata*, *Delosperma aberdeenense*, *Haworthia marumiana* and what are probably the southernmost populations of *Mossia intervallis*. All of these are plants typical of relatively high altitudes (occurring here at about 1 700 m) and exhibiting a strong tolerance for frost.

Huernia piersii has also been found in reasonable numbers on a similar formation (i.e. almost bare dolerite domes) to the east of Steynsburg, again at an altitude of about 1700 m. Here succulents abounded (in contrast to the situation in the surrounding veld, where they were quite rare), with *Duvallia caespitosa* and *Stapelia grandiflora*, *Neohenricia sibettii*, large numbers of *Euphorbia pulvinata* and *Sarcocaulon salmoniflorum*, among many others.

Diagnostic features and relationships

In plants from near Sterkstroom and Steynsburg the corolla is spotted and transversely dashed with red-brown to maroon on a cream to faintly greenish background, with the spots becoming transversely longer (and consequently the corolla darker) towards the mouth of the tube. Inside the tube they coalesce into several concentric dark circles. The tube is relatively shallow (at least broader than long) and usually slightly constricted at the mouth, while the lobes spread out fully at its mouth or are even slightly recurved. Dark maroon bristles are present in the mouth of the tube and extend onto the lower parts of the corolla lobes but rapidly fade away into very small papillae.

In the key, Leach (1988: 13) separated *H. brevirostris* (= *H. thuretii*) and *H. piersii* as follows:

Corolla bicampanulate with long (up to 2.5 mm) outstanding clavate subclavate or simple straight hairs in and around the concentrically lined and spotted tube = *H. piersii*
Corolla almost rotate, with a shallow tube and widely spreading limb, papillae usually tipped with a short acute bristle or apiculus = *H. brevirostris*

Plants of *H. piersii* from near Sterkstroom and Steynsburg have an almost rotate corolla with a relatively shallow central tube. That it is not generally bicampanulate can be seen clearly in fig. 9 of Leach (1988) and in the figures that are shown here. The tube is much shallower than is usual in *H. barbata* but is comparable in depth with that in *H. thuretii*. *Huernia piersii* and *H. thuretii* differ by the nature of the papillae on the surface of the corolla: in *H. piersii* they are relatively short and each is tipped, at least in the mouth of the tube and on the bases of the

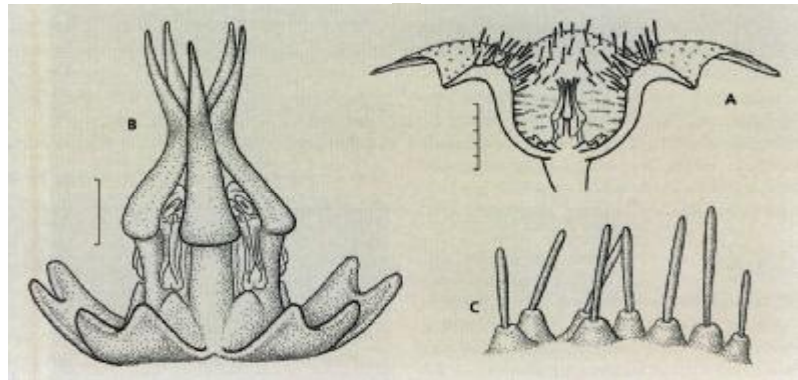


Fig. 5.129. *Huernia piersii*. A, side view of dissected flower. B, side view of gynostegium. C, papillae inside corolla in mouth of tube. Scale bars: A, 5 mm; B, C, 1 mm (at B). Drawn from PVB 5039, near Sterkstroom.



Fig. 5.130. *H. piersii*, PVB 1763a, north of Graaff-Reinet (though possibly a hybrid between *H. barbata* and *H. thuretii*).

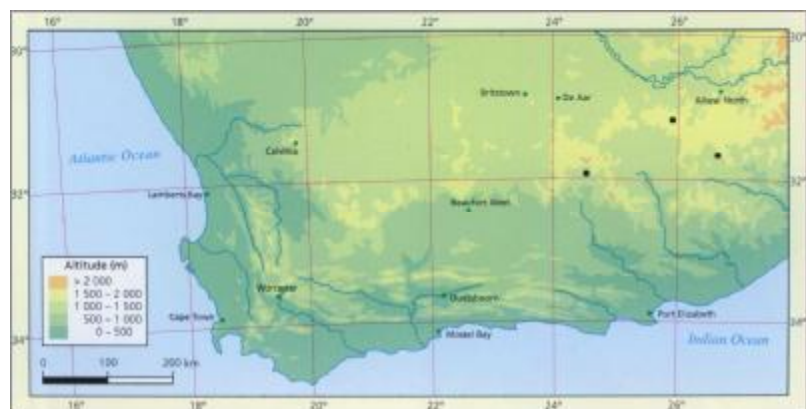


Fig. 5.131. Distribution of *Huernia piersii*.

HUERNIA GUTTATA

lobes, with a long, outstanding bristle; in *H. thuretii* the papillae may be a little taller but the apical bristle is much reduced and rarely exceeds 1 mm long.

Huernia piersii shares with *H. barbata* the relatively long bristles on the papillae. It differs from *H. barbata* in the length of the tube (which is shorter and relatively broader) and the manner in which the lobes spread out fully beyond it.

History

Huernia piersii was discovered by Charles Presgrave Piers in May 1906. Piers was born in Rondebosch, Cape Town, in August 1885 and became the Government Land Surveyor in the then Rhodesia, dying in Harare on 29 July 1962. He is also the discoverer of *Aloe inyangensis* (Reynolds 1966).



Fig. 5.132. *H. piersii*, PVB 5039, near Sterkstroom. As these pictures show, the colour of the flowers is very variable at this place, which is the type locality.



Fig. 5.133. *H. piersii*, PVB 5039, near Sterkstroom.



Fig. 5.134. *H. piersii*, PVB 5039, near Sterkstroom.

19. *Huernia guttata*

Huernia guttata (Masson) Haw., Syn. Pl. Succ.: 30 (1812).

Stapelia guttata Masson, Stap. Nov.: 10, t. 4 (1796).

Type: South Africa, Masson (missing).

Lectotype: Masson, Stap. Nov.: t. 4.

Small succulent forming clump 60-200 mm diam. Stems 20-100 mm long, 10-15 mm thick, decumbent, grey-green, sometimes mottled with purple-red; tubercles 4-8 mm long, deltoid, spreading, laterally flattened and joined into 4-5 angles along stem. Inflorescence of 1-3 flowers developing in gradual succession on short peduncle (< 5 mm long) with slender lanceolate bracts 2-4 mm long; pedicel 10-30 mm long, 2 mm thick, spreading with upturned apex holding flower facing upwards; sepals 5-7 mm long, 2 mm broad at base, narrowly ovate-acuminate. Corolla (20-) 25-70 mm diam., shallowly bowl-shaped to rotate; outside smooth, pale reddish on cream, with 1-3 raised longitudinal veins on each lobe running down towards tube; inside cream with red to maroon spots becoming larger on annulus and coalescing into solid red/maroon in tube (tube sometimes transversely lined or spotted with red or maroon towards base then coalescing around corona), annulus smooth except for some obtuse conical papillae in mouth of tube each bearing erect cylindrical to clavate apical bristle 2.5-4.0 mm long (minute acute papillae on lobes and around corona); tube $\pm$ 6 mm long, 10 mm broad at mouth, cupular, cylindrical, corolla slightly thickened into shiny annulus around mouth (annulus consisting of slightly thickened tissue pushed forward below bases of lobes); lobes $\pm$ 8-10 mm long, 15 mm broad at base, erect to spreading or recurved, broadly deltate, acuminate. Corona 6-8 mm tall, 4.5-8.0 mm broad, without basal stipe; outer lobes subquadrate to oblong, emarginate to deeply bifid, spreading on base of tube and partially fused to it, cream to maroon; inner lobes $\pm$ 4 mm long, adpressed to backs of anthers towards base then connivent-ascending and diverging, below slightly dorsiventrally flattened with slightly inflated dorsal gibbosity at base, above terete and tapering to slender apex, cream blotched with maroon.

Huernia guttata is widespread, occurring in widely scattered areas from the Suurberg in the Eastern Cape to southern Namagaland.

Vegetatively the plants in the southern and Eastern Cape have a slightly different appearance from those in the Western Cape. The former have only slightly mottled, 4-angled stems, while in the west the stems are nearly always 5-angled and are brightly mottled with purple-red on green. In plants from around the Calitzdorp Dam the stems are also often 5-angled but they are quite without the bright mottling found further west.

According to Leach, in *H. guttata* the tube is shallow and lacks small bristles below the larger ones in the mouth; on the other hand in *H. reticulata* the tube was '± as long as wide, beset with short stiff hairs below the inwardly pointing long hairs at the mouth' (Leach 1988: 14). However, in many plants of *H. guttata* the tube is only slightly broader than long and in some from near Willowmore (e.g. PVB 7070) there are small bristles towards the base of the tube. Leach (1988: 42) also mentioned the 'tall staminal column' but, as can be seen from the illustrations here, there are no obvious differences in the lengths of the columns in western and eastern material. There seem to be no grounds on which one could recognise two species here and the only more or less reliable means of distinguishing them are the different colour of the stems and the denser concentration of bristles in the mouth of the tube.

Just as there seems to be no basis for recognising *H. reticulata* as distinct from *H. guttata*, there is no reason to uphold subsp. *calitzdorpensis* L.C. Leach. This was separated from subsp. *guttata* by the 'larger and darker' flowers 'with the tube usually solidly dark maroon, only occasionally with some obscure transverse yellowish lineations'. Material collected recently along the Kouga River and around Joubertina (which is where material

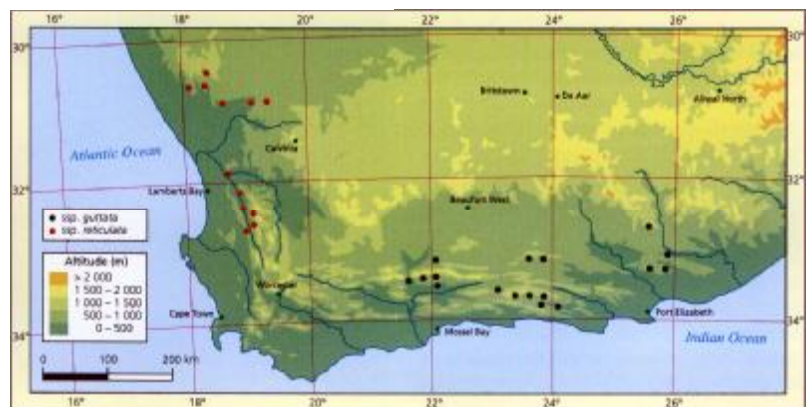


Fig. 5.135. Distribution of *Huernia guttata*.

came from that Leach considered most typical of subsp. *guttata*) is as dark as any seen around Calitzdorp and in fact some have a nearly uniformly dark maroon annulus without any spotting (fig. 5.136). Some of these collections also have flowers up to 55 mm diameter and these easily match flowers from the Calitzdorp area in size too.

Key to the subspecies of *H. guttata*

Stems 4-5-angled and $\pm$ uniformly coloured, corolla tube with scattered bristles in mouth 19a. subsp. *guttata*

Stems 5-angled and mottled with purple-red, corolla tube with fairly dense beard of bristles in mouth 19b. subsp. *reticulata*



Fig. 5.136. *H. guttata* subsp. *guttata*, PVB 7095, near Kareedouw.

19a. *Huernia guttata* subsp. *guttata*

Stapelia venusta Masson, Stap. Nov.: 10, t. 3 (1796).
Huernia venusta (Masson) Haw., Syn. Pl. Succ: 29 (1812).

Type: South Africa, Masson (missing).
Lectotype: Masson, Stap. Nov.: t. 3.

Stapelia lentiginosa Sims, Bot Mag. 15: t. 505 (1801);
Huernia lentiginosa (Sims) Haw., Syn. Pl. Succ: 29 (1812).

Lectotype: Bot. Mag.: t. 505.

Stapelia ocellata Jacq., Stap.: t. 6 (1806-19).

Huernia ocellata (Jacq.) Schult. in Roem. & Schult., Syst. Veg. 6: 9 (1820).

Lectotype: Jacq., Stap.: t. 6.

Stapelia venusta Jacq., Stap.: t. 7 (1806-19), non Masson (1796).

Lectotype: Jacq., Stap.: t. 7.

Stapelia venusta var. *minor* Jacq., Stap.: t. 64, fig. 4 (1806-19).

Lectotype (selected here): Jacq., Stap.: t. 64, fig. 4
Huernia guttata subsp. *calitzdorpensis* L.C. Leach, Excelsa Taxon. Ser. 4: 38 (1988).

Type: Calitzdorp Dam, Leach & Roussouw 16147 (NBG).

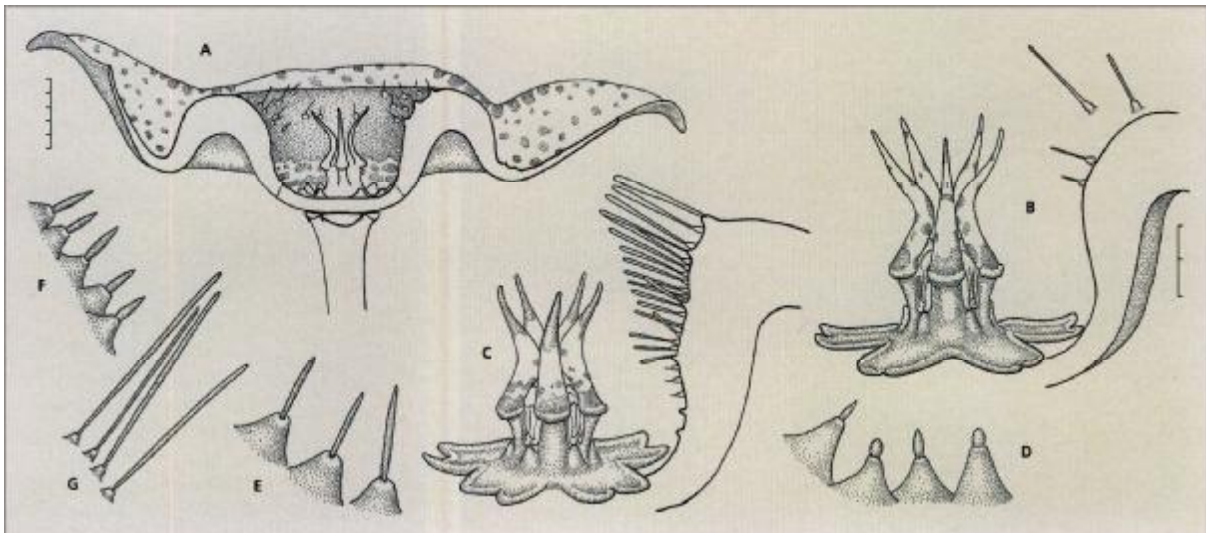


Fig. 5.137. *Huernia guttata* (A, B, D-F, subsp. *guttata*; C, G, subsp. *reticulata*) A, side view of dissected flower. B, C, side view of gynostegium with part of corolla tube. D-G, papillae inside corolla at mouth of tube. Scale bars: A, 5 mm; B, C, 2 mm (at B); D-G, 1 mm (at B). Drawn from A, D, PVB 7095, near Kareedouw; B, PVB 7080, Saptou; C, PVB 6819, west of Loeriesfontein; E-F, PVB 7137 (different flowers), Tweeriviere, Kareedouw; G, Aslander, north of Clanwilliam.

HUERNIA GUTTATA

Stems 4-5-angled, uniformly grey-green to very faintly mottled with purple. Corolla tube with scattered bristles in mouth.

Distribution and habitat

Subsp. *guttata* has been recorded from near Somerset East and in the Suurberg, to around Willowmore. It is also known between Uniondale and Joubertina in the Longkloof and further to the west between Oudtshoorn and Calitzdorp.

Plants of subsp. *guttata* are often of very

scattered occurrence and invariably grow on stony slopes under bushes. In the eastern part of the distribution they are often associated with sandstone mountains and, for example in the Suurberg and in the Longkloof, they grow on north-facing slopes in semi-arid spots with shallow soils overlaying rock slabs surrounded by *fynbos* elements. In such spots they often cohabit with various species of *Crassula* and *Haworthia*. In the west around Calitzdorp and Oudtshoorn specimens are usually found on dry, shale slopes under short shrubs of *Rhigozum* and other karroid species.

Diagnostic features and relationships

In subsp. *guttata* the flower is very striking indeed. It is usually comparatively large and has a broad, flattish area outside the tube. Around the mouth of the tube the corolla is thickened and strongly reflexed and this combination gives it a prominent annulus there. The annulus is dull to shiny and differently coloured to the rest of the corolla, usually with bold red to maroon spots that coalesce towards the mouth of the tube and become smaller towards the lobes. The lobes are pale yellow with fine red to maroon spots and are covered with fine papillae. The tube has a number of larger papillae near the mouth, each of which is tipped with a clavate bristle but these fade out on the annulus. Subsp. *guttata* lacks the generally much denser collection of these bristle-tipped papillae in the tube that one finds in subsp. *reticulata*.

History

Stapelia guttata was discovered by Francis Masson but it is not known where he first found it. The relatively long buds, the comparatively large flower and the colouring suggest that Masson's *Stapelia venusta* may also be subsp. *guttata* and it is included here in its synonymy.



Fig. 5.138. *H. guttata* subsp. *guttata*, PVB 4945, just west of Miller siding.



Fig. 5.139. *H. guttata* subsp. *guttata*, PVB 7070, Trompetterspoort, north-east of Willowmore.



Fig. 5.140. *H. guttata* subsp. *guttata*, PVB 7137, near Joubertina.

19b. *Huernia guttata* subsp.
reticulata

Huernia guttata subsp. *reticulata* (Masson)

Bruyns, *comb. et stat. nov.*

Stapelia reticulata Masson, *Stap.* Nov.: 9, t. 2 (1796).

Huernia reticulata (Masson) Haw., *Syn. Pl. Succ.*: 28 (1812).

Type: South Africa. Olifants River Valley, Masson (missing).

Lectotype: Masson, *Stap.* Nov.: t. 2.

Stapelia reticulata var. *deformis* Jacq., *Stap.*: t. 9 (1806-19).

Lectotype (selected here): Jacq., *Stap.*: t. 9.

Stapelia crassa J.Donn ex Haw., *Syn. Pl. Succ.*: 28 (1812).

Type: unknown.

Stems 5-angled, usually brilliantly mottled with purple-red on grey-green. Corolla tube with fairly dense beard of bristles in mouth.

Distribution and habitat

Subsp. *reticulata* is recorded in the Western Cape, from southern Namaqualand to the Olifants River Valley. In this region it occurs from Garies eastwards to near Loeriesfontein and from Klawer to Citrusdal along the valley of the Olifants River.

In southern Namaqualand plants are found on gneiss slopes under small bushes with a wealth of other small succulents belonging to the succulent Aizoaceae and the Crassulaceae. In the Olifants River Valley they grow in locally semi-arid spots in shallow soils on sandstone slabs, often with various black lichens, *Conophytum obcordellum*, other succulent Aizoaceae such as species of *Antimima* and *Oscularia* and *Euphorbia loricata*. These spots are surrounded by dry fynbos or elements of the Succulent Karoo.



Fig. 5.142. *H. guttata* subsp. *reticulata*, PVB 1342, east of Garies.

Diagnostic features and relationships

In subsp. *reticulata* the stems are nearly always very strikingly mottled with purple on a grey-green background. They often also have the angles slightly spiralling along the stem, but not to anything like the extent to which this is seen in *H. nouhuysii*.

In southern Namaqualand subsp. *reticulata* has flowers very similar to those from the Eastern Cape. Most of the inside of the flower is covered with a beautiful mottling of irregular red spots on a cream background which becomes shiny with much larger, rounder deep red or

maroon spots on cream on the annulus.

In the Olifants River Valley the flowers are even more intensely coloured. Here the deep maroon of the 'annulus' extends to the lobes which are only finely reticulated with yellow rather than yellow with fine red dots. These plants have been known traditionally as *H. reticulata*.

History

Francis Masson discovered his *Stapelia reticulata* on rocks along what he called the 'northern Olifants River' which is possibly near where Klawer is located today.



Fig. 5.141. *H. guttata* subsp. *reticulata*, PVB 6819, west of Loeriesfontein.



Fig. 5.143. *H. guttata* subsp. *reticulata*, PVB, Olifants River Valley, north of Citrusdal.

HUERNIA TRANSVAALENSIS

20. *Huernia transvaalensis*

Huernia transvaalensis Stent, *Bull. Misc. Inform.*
1914: 249 (1914).

Type: South Africa, Transvaal, Crocodile Poort, Pole
Evans (PRE).

Small succulent forming clump 150 mm-1 m diam. Stems 20-120 mm long, 10-15 mm thick (excluding teeth), decumbent, grey-green occasionally marked with purple; *tubercles* 5-8 mm long, deltoid, spreading, laterally flattened and joined into 4-5 wing-like angles along stem, tapering to small acute teeth. *Inflorescence* of 1-5 flowers developing in gradual succession from short stout peduncle (up to 5 mm long) with slender lanceolate bracts 2-4 mm long; *pedicel* 20-25 mm long, 2 mm thick, spreading with ascending apex holding flower facing $\pm$ upwards; *sepals* 8-10 mm long, 1.0-1.5 mm broad at base, ovate, attenuate. *Corolla* 45-55 mm diam., shallowly bowl-shaped to rotate; outside smooth, greenish cream mottled with red (not corresponding with inside colouring at all) with 1 heavy raised longitudinal vein running down centre of each lobe; inside transversely lined with red to maroon on cream to yellowish background on lobes and base of annulus becoming shiny red to maroon on annulus and in tube, with obtuse conical papillae in upper half of tube to particularly around mouth each bearing obtuse cylindrical bristle up to 4 mm long (minute slender sharp papillae on lobes); *tube* 5-7 mm long, 8-10 mm broad at mouth, cupular, cylindrical, mouth bounded by raised annulus (annulus consisting of slightly thickened tissue pushed forward above bases of lobes); *lobes* 12-15 mm long, $\pm$ 20 mm broad at base, spreading, deltate, acuminate. *Corona* 4.5-5.0 mm tall, 6-7 mm broad, without basal stipe; *outer lobes* 1.5-2.0 mm long, shortly to deeply obtusely bilobed, cream with maroon margin, spreading on base of tube and fused to corolla for at least half of length; *inner lobes* $\pm$ 3 mm long, yellow with maroon margins and apex, adpressed to backs of anthers near base then rising above them, becoming connivent and slightly divergent towards apex, tapering from transverse dorsal gibbosity to slender and smooth apex.

Distribution and habitat

Huernia transvaalensis is primarily found from Ellisras in Limpopo Province south-eastwards to Pretoria and Marble Hall. There is an isolated record from Vryburg in North-West Province. It seems generally to be uncommon and there are usually only few, scattered plants in a particular locality.

Plants occur in flat areas among trees and grasses, occasionally on stony ground and on hills.

Diagnostic features and relationships

The stems of *H. transvaalensis* are stout and very strongly 4- or 5-angled and may form clumps up to 0.5 m or more in diameter.

As in many of the *Huernias* with an annulus on the corolla, the flowers of *H. transvaalensis* are very brightly coloured and pretty and they are also fairly large. In *H. transvaalensis* the corolla is generally about 50 mm in diameter and relatively flat with a short, cupular tube in the centre. On the lobes and the outer edge of the 'annulus' it is heavily transversally marked with red to maroon on a cream background, becoming plain and somewhat shiny red to maroon on the 'annulus' and in the tube. Within the tube there are long, slender bristles, each of which arises from a short papilla. Outside the tube the 'annulus' is glabrous but the lobes are covered with minute, sharp-tipped papillae.

The broad outer corona of *H. transvaalensis* is usually cream with maroon along the edge and the lobes spread on the base of the tube. The inner corona consists of slender lobes which are connivent in the centre, then rise above the anthers and taper to fine points.

Huernia transvaalensis differs from *H. zebrina* (which occurs to the north and west of it and looks very similar florally) in having much

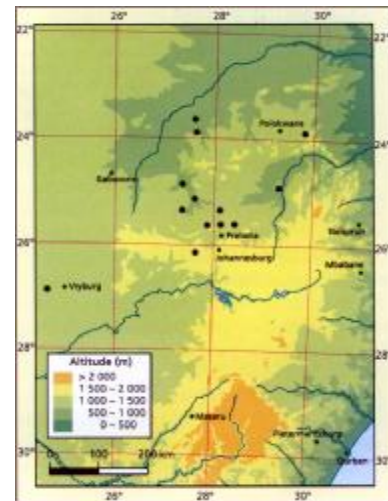


Fig. 5.144. Distribution of *Huernia transvaalensis*.

less regularly arranged dark bars on the corolla lobes and, more importantly, by the much longer inner corona lobes which taper to a fine, slender point. It seems that the closest relatives are *H. guttata* in the Eastern and Western Cape and *H. erectiloba* in northern Mozambique. From *H. guttata*, *H. transvaalensis* differs in that the red or maroon in *H. transvaalensis* forms bands against the cream background while in *H. guttata* it forms more or less circular dots on the cream background. The inner corona lobes in *H. transvaalensis* are also shorter than in *H. guttata* where they are never yellow either. *Huernia erectiloba* differs in having a somewhat papillate exterior to the corolla, a longer corolla tube, spots rather than transverse bands on the lobes inside, and longer inner corona lobes.

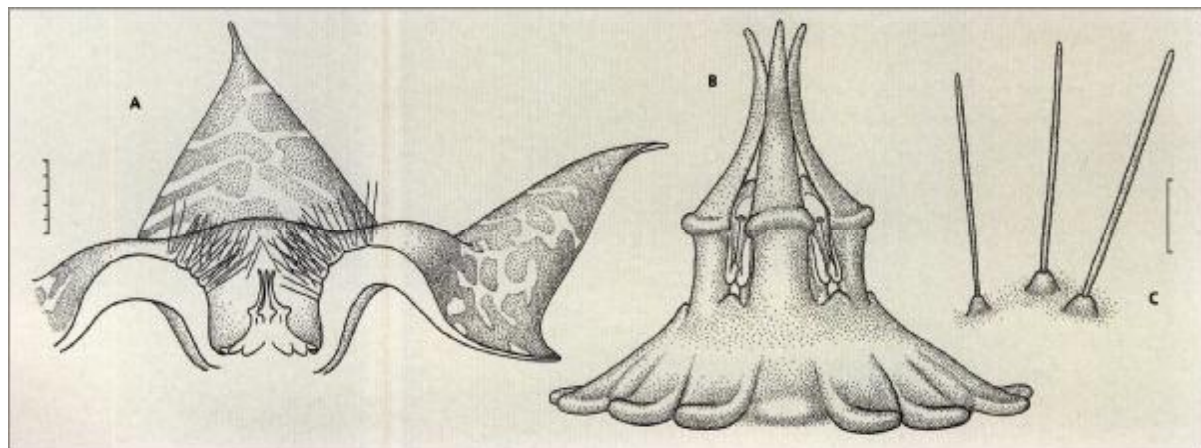


Fig. 5.145. *Huernia transvaalensis*. A, side view of dissected flower. B, side view of gynostegium. C, papillae inside corolla at mouth of tube. Scale bars: A, 5 mm; B, C, 1 mm (at C). Drawn from PVB 6544, south of Ellisras.

History

Huernia transvaalensis was discovered by I.B. Pole-Evans on 24 August 1913 at Crocodile Poort, which lies in the Magaliesberg near Rustenburg.



Fig. 5.146. *H. transvaalensis*, PVB 6544, south of Ellisras.



Fig. 5.147. *H. transvaalensis*, PVB 6544, south of Ellisras, flower with unusually fine markings, in habitat, January 1996.

21. *Huernia erectiloba*

Huernia erectiloba L.C. Leach & Lavranos, *Kirkia* 3: 38 (1963).

Type: Mozambique, Niassa Prov., ± 45 km east of Ribaua, Leach and Rutherford-Smith 10914 (SRGH, holo.; PRE, MO, iso.).

Succulent forming dense to loose clumps up to 1 m diam. Stems 50-100 (-200) mm long, 4-12 mm thick, decumbent, pale grey-green flecked with purple; tubercles 2-6 mm long, spreading, deltoid, laterally slightly flattened and joined into 4 or 5 angles along stem, tapering abruptly to subulate leaf-rudiment 1-2 mm long. Inflorescence of 1-3 flowers developing in gradual succession from short peduncle, with slender bracts; pedicel 10-20 mm long, ± 1.5 mm thick, spreading with ascending apex to hold flower facing upwards; sepals 5-7 mm long, 1.5 mm broad at base, attenuate. Corolla 22-30 mm diam., bicampanulate; outside finely papillate, cream spotted with red; inside cream with red to maroon spots becoming larger on annulus and coalescing into solid shiny red to maroon in tube, with low mound-like papillae on annulus and in mouth of tube each bearing erect cylindrical bristle to 2 mm long (minute papillae on lobes and united area beyond annulus); tubes 10 mm long, 7-10 mm broad at mouth, cupular, sometimes thickened and usually slightly constricted in middle, corolla thickened into low shining annulus around mouth; lobes 5-8 mm long, 11 mm broad at base, erect and recurved towards apices, broadly deltate, acuminate. Corona 5-7 mm tall, 5-6 mm broad, without basal stipe; outer lobes subquadrate to shortly bifid, spreading on base of tube and partially fused to it, yellow to cream with maroon margins; inner lobes 3.5-4.5 mm long, adpressed to backs of anthers towards base then connivent-ascending and diverging, below slightly dorsi-

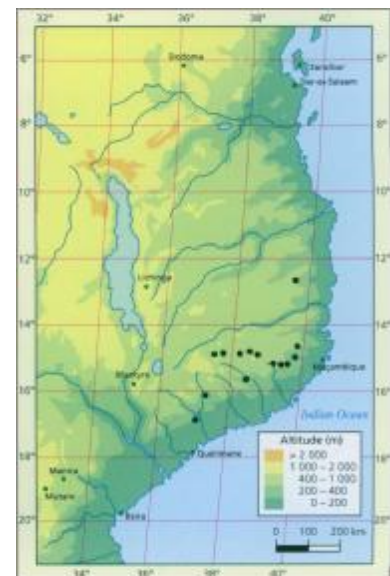


Fig. 5.148. Distribution of *Huernia erectiloba*.

HUERNIA ERECTILOBA



Fig. 5.149. *H. erectiloba*, PVB 7693, south of Errego, Zambésia Province, Moçambique.



Fig. 5.150. *H. erectiloba*, PVB 7693, south of Errego, Zambésia Province, Moçambique.



Fig. 5.151. *H. erectiloba*, PVB 7713, east of Nampula, Nampula Province, Mocambique.

ventrally flattened with only very slightly inflated dorsal gibbosity at base, above terete and tapering to slender apex, cream mottled with red.

Distribution and habitat

Huernia erectiloba is known in the Cabo Delgado, Nampula, Niassa and Zambésia provinces of northern Moçambique. Here records extend from about 200 km north of the Zambezi River near Mocuba northwards to Nampula and westwards to around Malema. It has also been located much further north near Quissanga, about 150 km south of the Tanzanian border. In most of these areas, while there is a wide variety of species of succulent *Euphorbia* and some species of *Ceropegia*, *H. erectiloba* is the only stapeliad present. Some of these parts receive a surprisingly high rainfall and, for example, south of Nampula *H. erectiloba* grows in a region receiving 1 400-1 800 mm of rain annually (Jackson 1961). Altitudes at which it occurs range from 200 to 1 200 m.

Plants of *H. erectiloba* grow exclusively on flattish to quite steeply sloping granitic domes (fig. 55-56) in shallow mats of black, peat-like

soil held together by a dense and tightly woven mass of roots. The dominant component on these soil-mats consists of various species of *Xerophyta*, the coarse, tough, dense, perennial, tussock-forming sedge *Coleochloa* and *Myrothamnus flabellifolius*. Nevertheless, succulents abound on them too and quite often become more plentiful than the non-succulent component. These include *Aloe cameronii*, *A. chabaudii*, *A. mawii*, *Ceropegia nilotica*, several species of spiny succulent *Euphorbia* such as *E. corniculata*, *E. grandicornis* and *E. ramulosa*, *Kalanchoe elizae* and *Sarcostemma viminalis*. There is also a wide selection of orchids, many of them epiphytic on the stems of *Xerophyta* or *Euphorbia* or lithophytic. Here *H. erectiloba* may be found sheltering under shrubs or growing in the open.

Diagnostic features and relationships

Specimens of *H. erectiloba* can reach 1 m in diameter and such plants consist of hundreds of stems. These are erect and packed tightly in exposed specimens but can be spreading and

very loosely clustered when they grow in more sheltered spots. Exposed stems always have a patchwork of purple blotches on a pale grey-green background.

The stems are 4- or 5-angled but the angles are thick and not particularly wing-like. Those which are 4-angled often have an almost square cross-section that is not otherwise known in *Huernia*.

In *H. erectiloba* the flowers are quite noticeably papillate outside. In the bud the top of the corolla becomes remarkably flat or even depressed just before anthesis. The relatively long, intermediate folds at the bases of the lobes arise quite close to the centre and point inwards. When the flower opens it has a tube that is considerably longer than broad. This is surrounded at its mouth by an almost flat, annulus-like area which is only slightly thicker than the fabric of the tube. There is often a thinner ring in the tube just below the annulus. Around the edge of this slight annulus the fused part of the corolla rises in a secondary bell with the short lobes spreading slightly around its mouth. Both this upper bell and the annulus are covered with large maroon spots

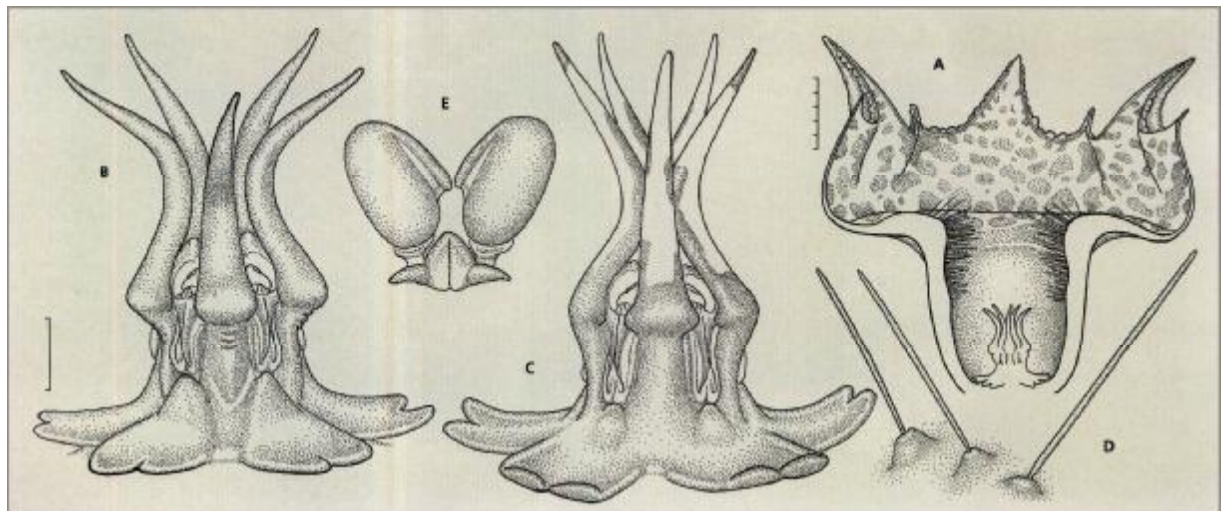


Fig. 5.152. *Huernia erectiloba*. A, side view of dissected flower. B, C, side view of gynostegium. D, papillae inside corolla on annulus. E, pollinarium. Scale bars: A, 5 mm; B, C, 1 mm (at B); D, 0.5 mm (at B); E, 0.25 mm (at B). Drawn from PVB 7693, south of Errego, Zambesia Province, Mocambique.

on a cream background, while the inside of the tube is dark maroon and shiny. One peculiarity of the flower of *H. erectiloba* which has not been seen in any other species of *Huernia* is the pale, papillate ridge of tissue that lines the margins of the lobes on the outside and is clearly visible in the buds. The flowers emit a slight excrement-like odour.

The gynostegium in *H. erectiloba* is amongst the tallest found in *Huernia*, with particularly long and slender inner lobes. Most of it is pale yellow spotted with maroon.

History

Huernia erectiloba was first recorded in 1937 by the Portuguese pharmacist and botanical collector Antonio Rocha da Torre near Nampula. Material was gathered next in May 1961 by Leach and R. Rutherford-Smith during one of Leach's extensive expeditions to northern Mozambique to investigate various species of *Euphorbia* and it was on the basis of this material that the species was described in 1963.



Fig. 5.153. *H. erectiloba*, PVB 7713, east of Nampula, Nampula Province, Mocambique, in habitat, December 1998.



Fig. 5.154. *H. erectiloba*, PVB 7713, east of Nampula, Nampula Province, Mocambique. A large plant, growing on a low, granite dome among sedges and *Xerophyta*, with a small plant of *Euphorbia corniculata* in the centre.

22. Huernia praestans

Huernia praestans N.E.Br., *Fl. Cap.* 4 (1): 914 (1909).

Type: South Africa, near Wittepoort between Ladismith and Laingsburg, *N.S. Pillans 667* (K, holo.; BOL, iso.)

Small succulent forming clump 50-300 mm diam. **Stems** 10-50 mm long, 7-10 mm thick (excluding teeth), decumbent to erect, grey-green; **tubercles** 3-5 mm long, spreading, deltoid, slightly laterally flattened and joined towards base into 4-5 angles along stem, tapering gradually into slender tooth. **Inflorescences** 1 per stem arising near base, of 1-5 flowers developing in gradual succession from short peduncle with small lanceolate bracts 1-2 mm long without lateral teeth; **pedicel** 4-12 mm long, 1.5 mm thick, ascending to hold flower facing partly upwards; **sepals** 3-6 mm long, 1.5 mm broad at base, narrowly acuminate. **Corolla** 35-55 mm diam., rotate with small tube in centre; outside smooth, cream suffused or lightly spotted with red, with 3 raised darker longitudinal veins along each lobe; inside cream to pale yellow, on sides of tube and around mouth irregularly transversely spotted or concentrically lined with maroon, solid maroon in base of tube, covered on lobes and annulus and inside mouth of tube with obtuse conical papillae each tipped with a clavate to nearly globose dark maroon bristle (together up to 1.5 mm long); **tube** 5-8 mm long, 7-8 mm broad at mouth, cupular, pentagonal, mouth emphasised by raised slightly thickened annulus (forced upwards by strong reflexion of corolla below lobes); **lobes** 7-9 mm long, 11-13 mm broad at base, spreading to reflexed, deltate, acute, often very slightly convex above but margins not folded back. **Corona** 4-5 mm tall, $\pm$ 4 mm broad, pale yellow spotted with maroon, without basal stipe; **outer lobes** 1-2 mm long, rectangular, emarginate to obtusely bilobed, spreading on base of tube and partly fused to it; **inner lobes** $\pm$ 3 mm long, adpressed to backs of anthers then rising somewhat connivent above them and then recurved, subulate, sometimes with dorsal gibbosity at base.

Distribution and habitat

Huernia praestans is only known in the Little Karoo. In the north it is found in the hills west of the Rooinek Pass and southwards to Wittepoort on the western edge of the Klein Swartberg. From here it extends fairly sporadically southwards and eastwards to the hilly areas around Ladismith and further south to near Muiskraal and around Vanwyksdorp.

Plants occur on stony slopes or flattish areas between small hills with hard, loamy soils. They usually grow well hidden under small bushes.

Diagnostic features and relationships

Specimens of *H. praestans* are usually small and often only 60-100 mm in diameter, though large plants up to 300 mm in diameter have been seen on occasion. In the field the stems are usually very short (frequently only 15 mm long) and could easily be mistaken for those of

HUERNIA PRAESTANS



Fig. 5.155. *H. praestans*, PVB 1404, just south of Ladismith.



Fig. 5.156. *H. praestans*, PVB 7119, south of Vanwyksdorp.



Fig. 5.157. *H. praestans*, PVB 7119, south of Vanwyksdorp.

Duvalia caespitosa if not examined carefully. The tubercles are arranged into five rows and, when the stems are turgid, there is often no groove at all between these rows. Only a few stems seem to have the angles arranged into four rows and this is probably restricted to the primary stem and one or two others.

The flower of *H. praestans* is indeed quite special, as the name implies, especially when compared to the modest stems. It is generally quite large (usually around 45 mm across) and is relatively flat, with a small, cupular tube in the centre, so that the pretty colouring of the inside is not hidden from view. The inside is pale yellow, with fine maroon spots which become larger near the mouth of the tube, thereby giving the centre of the flower a reddish hue. These spots mostly change into concentric lines in the tube, ending in a dark patch around the corona. There is a distinctly raised area around the mouth of the tube which, though varying from quite shiny to not at all shiny, is only slightly differently coloured (by its larger maroon spots) from the rest of the flower. It is very slightly thicker than the rest of the corolla and so forms an 'annulus' of sorts. This 'annulus' is covered densely with papillae, each of

which is tipped with a thick, clavate dark bristle up to twice as long as the basal papilla. These papillae are actually present all over the corolla outside the tube but are much smaller on the lobes and so are less obvious there than on the 'annulus'. Inside the tube they suddenly disappear just below the mouth and the rest of the tube is smooth. Another feature of the flowers (though variably present) is the peculiar radial ridge along the middle of each lobe; these are usually most prominent towards the base of the lobes just beyond the 'annulus'.

The corona consists of outer lobes adpressed to the base of the tube and inner lobes which taper to long, slender, fine tips,

spreading strongly above the centre to become nearly horizontal.

There is much similarity between *H. praestans* and hybrids found near Calitzdorp between *H. guttata* and *H. barbata*. The possible origin of this species as a hybrid exists but this has not been tested by pollination experiments.

History

Huernia praestans was discovered by N.S. Pillans in November 1904 near Wittepoort in the Little Karoo. It has never been a well-known species and even today it is not at all common in cultivation.

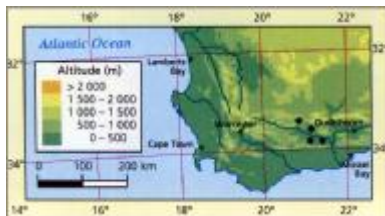


Fig. 5.158. Distribution of *Huernia praestans*.



Fig. 5.159. *H. praestans*, PVB 7119, south of Vanwyksdorp.

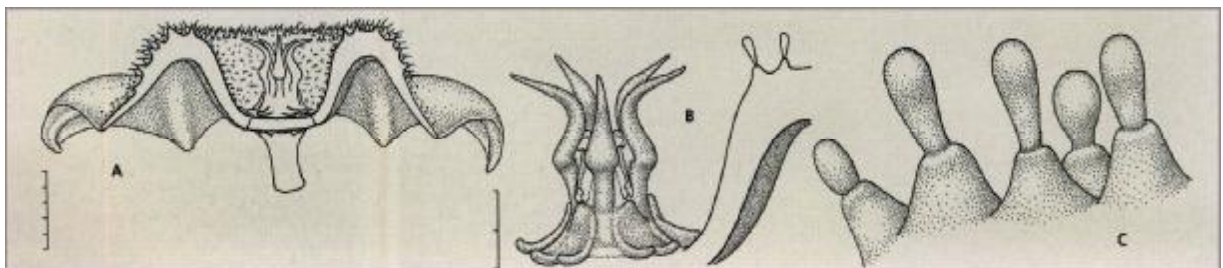


Fig. 5.160. *Huernia praestans*. A, side view of dissected flower. B, side view of gynostegium with part of corolla tube. C, papillae inside corolla in mouth of tube. Scale bars: A, 5 mm; B, 2 mm; C, 0.5 mm (at B). Drawn from PVB 7119, south of Vanwyksdorp.

23. *Huernia hystrix*

Huernia hystrix (Hook. f.) N.E.Br., Gard. Chron.

N.S. 5: 795 (1876).

Stapelia hystrix Hook. f., Bot. Mag. 95: t. 575! (1869).

Type: South Africa, Natal, Mcken (missing).

Lectotype: Bot. Mag.: t. 575!.

Small succulent forming spreading clump 60-300 mm diam. Stems 20-70 (-100) mm long, 8-10 mm thick, decumbent-ascending, pale green, often glaucous; tubercles 3-8 mm long, deltoid-acuminate, spreading, laterally flattened and joined towards base into 5 sometimes slightly spiralling angles along stem, often tapering into sharp, yellow-tipped spine 2-3 mm long. Inflorescence usually 1 per stem, of 1-3 flowers developing in gradual succession from lower half of stem on short peduncle (< 5 mm long) with few filiform bracts 5-7 mm long; pedicel 15-60 mm long, 2 mm thick, spreading with upturned apex holding flower facing upwards on ground; sepals 7-12 mm long, 1.0-1.5 mm broad at base, narrowly ovate-attenuate to filiform, obtusely keeled. Corolla 30-50 mm diam., ± rotate beyond mouth of tube; outside covered with conical obtuse papillae especially on tube, greenish cream suffused with pink, with 3-5 heavy

raised longitudinal veins running down each lobe; inside with concentric lines and dots of red-brown to maroon on cream, lines becoming finer and denser in tube and coalescing towards base, becoming coarser outside tube, covered from just inside mouth of tube to tips of lobes with obtuse columnar usually dorsiventrally flattened papillae, papillae marked with brown-red/maroon spots and lines, longest just outside mouth of tube (3.0-5.5 mm long) and often forming rows along margins of lobes, each with a minute apical bristle; tube 5-6 mm long, 10-12 mm broad at mouth, broadly cupular and slightly constricted at mouth by thickening in corolla, cylindrical; lobes 12-15 mm long, 12-15 mm broad at base, spreading to reflexed, deltate, acute to shortly attenuate. Corona 6-7 mm tall, 5-6 mm broad, without basal stipe; outer lobes 0.5-1.5 mm long, very short and ± rectangular (sometimes fused and nearly disc-like) to somewhat longer than broad, bifid to emarginate, spreading on base of tube and fused to it towards their base, cream often with maroon dots along margins to dark maroon; inner lobes ± 4 mm long, white to greenish cream towards base, maroon speckled on cream on upper swollen part, erect, dorsiventrally flattened and linear from a slightly dorsally gibbous base, abruptly expanded at apex into inverted ± foot- to hoof-shaped fleshy appendage.

A well-known and quite distinctive species, *H. hystrix* is widely distributed over the eastern side of tropical and subtropical southern Africa. It has been recorded from the North-West Province through southern Zimbabwe to coastal Moçambique near Vilankulo and Swaziland. Along the east coast of South Africa it occurs through KwaZulu-Natal as far south as Umtata in the Eastern Cape.

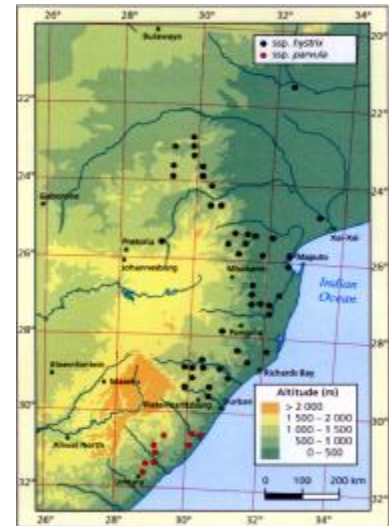


Fig. 5.161. Distribution of *Huernia hystrix*.

Key to the subspecies of <i>H. hystrix</i>	
Tubercles on stems with sharp yellow-tipped spine, pedicel 25-60 mm long, outer corona lobes up to 1 mm long, apex of inner lobes smooth and 1.5-2.0 mm long	23a. subsp. <i>hystrix</i>
Tubercles on stems without sharp yellow tip, pedicel 14-32 mm long, outer corona lobes ± 1.5 mm long, apex of inner lobes papillate and < 1 mm long	23b. subsp. <i>parvula</i>

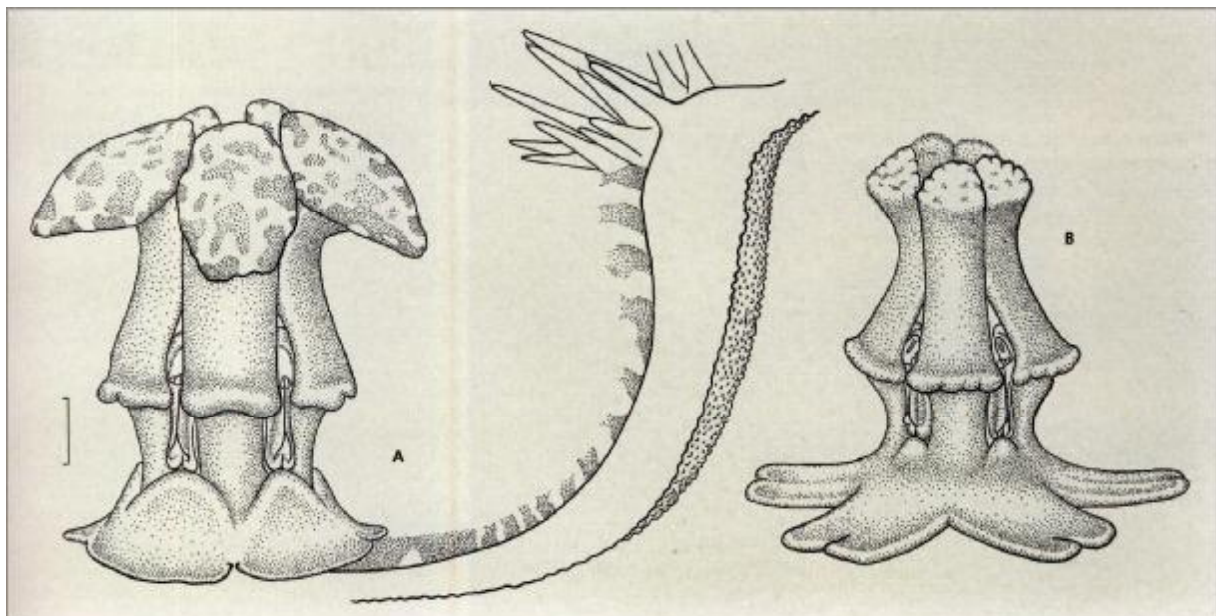


Fig. 5.162. *Huernia hystrix* (A, subsp. *hystrix*; B, subsp. *parvula*). A, B, side view of gynoecium (in A with part of corolla tube). Scale bars: A, B, 1 mm (at A). Drawn from A, PVB 6583, near Mara Siding, west of Louis Trichardt; B, PVB 4391, Tsitsa River, in the former Transkei.

HUERNIA HYSTRIX

Huernia hystrix is closely allied to such species as *H. volkartii* and *H. stapelioides*. It differs vegetatively from both: the stems are more spiky and stouter than in *H. volkartii* (though this is less clear for *H. hystrix* subsp. *parvula*) and they are 5-angled, unlike those of *H. stapelioides* which are always 4-angled. The flowers are generally borne on relatively long pedicels and are held facing upwards on the ground while in the others they tend to face outwards among the stems on short pedicels. Finally, the inner corona lobes in the others are apically bristly which is not the case for *H. hystrix* (again this is less clear for *H. hystrix* subsp. *parvula*, where the apices are somewhat papillate).

23a. *Huernia hystrix* subsp. *hystrix*

Huernia appendiculata A.Berger, *Stap. u. Klein.*: 174 (1910).

Huernia hystrix var. *appendiculata* (A.Berger)

A.C.White & B.Sloane, *Stap.*, ed. 2, 3: 898 (1937).

Type: South Africa (NY).

Stems 20-70 mm long; *tubercles* 4-8 mm long, usually tapering into sharp, yellow-tipped spike 2-3 mm long. *Pedicel*(20-) 25-60 mm long. *Corolla* 30-50 mm diam.; inside densely covered with prominent papillae up to 3.5-5.5 mm long. *Corona*; *outer lobes* 0.5-1.0 mm long, ± rectangular, emarginate, cream often with maroon dots along margins; *inner lobes* greenish cream towards base, maroon speckled on cream towards abruptly expanded inverted foot-shaped smooth apex 1.5-2.0 mm long.

Distribution and habitat

Subsp. *hystrix* is found widely in the northern most part of South Africa from around the foot of the Soutpansberg to near Barberton, in the south-eastern corner of Zimbabwe, in Moçambique from the south to as far north as near Vilankulo and in eastern Swaziland. It is also found extensively in KwaZulu-Natal from Ingwavuma southwards to the dry parts of the valley of the Tugela River.

Plants usually grow in leaf-litter somewhat sheltered under bushes or alongside trees in flat to gently sloping areas, often with species of *Aloe* and *Euphorbia*. In coastal Moçambique, near Vilankulo, they grow in thick leaf-litter on the floor of dwarf (2-3 m tall) *Brachystegia* forest, with many other small succulents.

Diagnostic features and relationships

Specimens of subsp. *hystrix* are usually somewhat diffuse and spreading, forming broad mats. The stems are usually noticeably spiny since the leaf-rudiment hardens into quite a long, sharp, yellow spike. In most areas this immediately separates it from any other species with which it might grow. However, in the valley of the Tugela River the stems are much

less obviously spiky and these hard yellow tips to the stems are absent.

In both subspecies the corolla has a relatively short tube, with lobes that often fold back behind the tube. The corolla is boldly marked with concentrically arranged, red-brown to maroon stripes, bars and dots on a cream background. These concentric lines are particularly noticeable on the more or less flat base of the tube. On the lobes and in the mouth of the tube they are made less obvious by the very prominent papillae, which may be over 5 mm long. These papillae abruptly disappear beneath the slight thickening in the corolla tube near its mouth.

The inner corona in subsp. *hystrix* is particularly distinctive and dominates the entire gynostegium. Each lobe is quite broad and somewhat flattened and has an especially

prominent apex which is usually shaped rather like an inverted foot. However, this is markedly less prominent in material from the valley of the Tugela River in KwaZulu-Natal.

History

Subsp. *hystrix* was first collected by Mark J. McKen and described as *Stapelia hystrix* by J.D. Hooker, who made the curious remark that 'at first sight it resembles so closely *Stapelia glanduliflora* that it was taken for that plant'.

In about 1876 N.E. Brown received cultivated material from J.E. Daniel of Epsom, England, and realised that this species belonged in *Huernia*. He commented on the large papillae of the corolla and the curiously shaped inner corona lobes which Hooker had also noticed.



Fig. 5.163. *H. hystrix* subsp. *hystrix*, PVB 6583, near Mara siding, west of Louis Trichardt.



Fig. 5.164. *H. hystrix* subsp. *hystrix*, PVB 4435, near Estcourt.

23b. *Huernia hystrix* subsp. *parvula*

Huernia hystrix subsp. *parvula* (L.C. Leach)

Bruyns, stat. nov.

Huernia hystrix var. *parvula* L.C. Leach, J. S. African

Bot. 42: 450 (1976).

Type: South Africa, Natal, Oribi Flats, Strey 9730
(PRE, holo.; K, MO, SRGH, iso.)

Stems 20-50 (-100) mm long; tubercles 3-5 mm long, tapering to acute tip. Pedicel 14-32 mm long. Corolla 30-35 mm diam.; inside with papillae up to 3 mm tall. Corona; outer lobes $\pm$ 1.5 mm long, rectangular, slightly bifid towards apex, dark maroon; inner lobes nearly white towards base, pale maroon towards truncate-clavate inverted hoof-like somewhat papillate and rugulose apex < 1 mm long.

Distribution and habitat

Subsp. *parvula* is found in the south-eastern corner of the distribution of the species from the vicinity of the Oribi Gorge in southern KwaZulu-Natal southwards to Umtata in the Eastern Cape.

Plants grow on dry, rather exposed, stony areas around the edges of sandstone cliffs and on rocks along river courses. They have also been observed a few times on doleritic outcrops growing in crevices on slabs of rock or in dry places under bushes between stones.

Diagnostic features and relationships

Although both subspecies have 5-angled stems, subsp. *parvula* will immediately be seen to be a much less prickly plant than the other and the tubercles are not tipped with a yellow spike but rather with an acute, greyish point which rapidly wears down. The stems are often very much smaller and, in many plants, are not more than 30 mm long, with specimens consisting of quite dense mats of these short stems. However, they can also be up to 100 mm long on occasion and even stouter and more robust than those of the typical subspecies.

The flowers in subsp. *parvula* are generally less strikingly coloured than those of subsp. *hystrix* and also rather less prominently papillate than in the typical, with the largest papillae mostly not more than 3 mm long. In plants from the Eastern Cape the corolla is finely dotted inside with maroon which coalesces into fine concentric rings towards the base of the tube and around the corona. Those from the Oribi Gorge and Izingolweni area are generally less boldly marked, especially towards the base of the tube, where they are often a uniform, pinkish red.

In subsp. *parvula* the outer corona lobes are always deep maroon and spread out on the base of the tube. The inner lobes are suffused with maroon becoming dark towards the apex. Their apices are distinctly less prominently swollen

than in subsp. *hystrix* and are hoof-like rather than foot-like. They are also finely papillate and somewhat rugulose above.

History

Subsp. *parvula* seems to have been gathered in the former Transkei first by Alfred G. McLoughlin in 1939. It was first recorded in the area around Oribi Gorge by R.A. Dyer in 1953 and, although at first suspected to belong to *H. volkarti* (Plowes 1971:16), it was eventually described as a variety of *H. hystrix* in 1976.

Leach (1976a; 1988) regarded 'var. *parvula*' as occurring only in the area around Oribi Gorge and placed various collections from further south in the former Transkei under 'var. *hystrix*'. However, living collections from these more southern localities have shown that, apart from the concentric lines in the base of the corolla tube which are more typical of subsp.



Fig. 5.165. *H. hystrix* subsp. *parvula*, PVB 4415, near Izingolweni, southern KwaZulu-Natal.

hystrix, they show all the characteristics in the stems, pedicels and inner corona of subsp. *parvula* and are included under it here. This taxon is distributed at least 200 km south of any other known locality for subsp. *hystrix* and, on account of this geographic separation, the rank of subspecies is the most appropriate.



Fig. 5.166. *H. hystrix* subsp. *parvula*, PVB 4391, Tsitsa River, in the former Transkei.



Fig. 5.167. *H. hystrix* subsp. *parvula*, PVB 4391, Tsitsa River, in the former Transkei.

24. *Huernia hislopil*

Huernia hislopil Turrill, Bull. Misc. Inform. 1922: 30 (1922).

Type: Zimbabwe, near Rusapi, *Hislop* (K).

Succulent forming clumps to 1 m diam. Stems 30-150 mm long, 8-12 mm thick (excluding teeth), decumbent, brownish or grey-green; tubercles 3-4 mm long, broadly deltoid, spreading, laterally flattened and joined into 5 slightly wing-like angles along stem, tapering abruptly to small acute tooth. Inflorescence of 1-5 flowers developing in gradual succession from short peduncle up to 5 mm long, with attenuate bracts 2-3 mm long; pedicel 6-25 mm long, 1.5 mm thick, spreading then ascending to hold flower facing upwards; sepals 6-10 mm long, 1.5-2.0 mm broad at base, narrowly ovate-acuminate. Corolla 40-50 (-60) mm diam., campanulate with distinct flat area outside tube below lobes; outside smooth, cream irregularly (sometimes very finely) spotted with pink, with 4-5 raised longitudinal veins running down each lobe onto tube; inside white to cream irregularly spotted with maroon changing abruptly to concentric maroon lines in lower half of tube (below thickening), papillate all over except below thickening in tube, papillae reaching max. length of 1 mm and densest towards mouth of tube then decreasing in length gradually onto lobes, papillae cream and spotted with maroon with short apical bristle; tube 10-15 mm long, 8-10 mm broad at mouth, broadest and hemispherical near base then narrowing towards distinct thickening $\pm$ halfway up, then $\pm$ cylindrical or gradually widening towards mouth, not pentagonal; lobes 12-22 mm long, 15-18 mm broad at base, spreading to somewhat recurved, deltate (longer than broad), acuminate to caudate. Corona 5.5-6.5 mm tall, 8-10 mm broad, without basal stipe; outer lobes spreading on base of tube and partly fused to it, divided into 5 broad $\pm$ truncate and emarginate lobes, dark maroon; inner lobes 4.0-4.5 mm long, cream spotted with pale maroon, with darker tips, adpressed to backs of anthers near bases then connivent-erect and becoming divergent above, below dorsiventrally flattened with inflated dorsal gibbosity at base, tapering to small obtuse finely tuberculate apex.

Key to the subspecies of *H. hislopil*

1. Corolla tube clearly swollen near base with upper portion of tube $\pm$ equal in length to swollen part, lobes mostly longer than broad, inner corona lobes not swollen at apex **24a. subsp. *hislopil***
1. Corolla tube slightly swollen near base with upper portion of tube longer than swollen part, lobes at most as long as broad, inner corona lobes slightly swollen at apex **2.**
2. Papillae inside corolla with apical bristle up to as long as papilla **24c. subsp. *cashelensis***
2. Papillae inside corolla with apical bristle always much shorter than papilla **24b. subsp. *robusta***

Leach & Plowes (1966a) first considered the problems presented by *H. hislopil*, *H. kirkii* and *H. longituba*. In this account, they cleared up the considerable confusion that had existed in the literature involving these names and, for the first time, gave some idea of their relative distributions. They also considered other taxa in this complex which their own collecting had brought to light and tried to place them in the context of these three species. This resulted in the description of *H. occulta*, *H. hislopil* subsp. *robusta* and *H. longituba* subsp. *cashelensis*.

Leach (1976a; 1988) subsequently treated the same species in broader contexts and the quite extensive lists of differences given in Leach & Plowes (1966a) gradually seem to have been whittled down, one presumes by the variability noted in a steadily wider range of collections. These differences appear to have crystallised to the following (summarised from Leach 1988):

H. hislopil: corolla tube distinctly swollen ('excalvated') in base, spotted and lined to base; papillae inside corolla mottled; inner corona lobes obtuse at apex but not swollen.

H. kirkii: corolla tube sometimes slightly swollen in base, spotted above becoming solid blackish maroon in base; papillae maroon; inner corona lobes distinctly swollen towards apex.

H. longituba: corolla tube not swollen in base, spotted and lined to base; papillae mottled; inner corona lobes distinctly swollen towards apex.

H. occulta: corolla tube slightly swollen in base, spotted above becoming solid dark maroon in base; papillae somewhat mottled; inner corona lobes arising exceptionally low on gynostegium, tapering to their tips.

However, the position is not actually as clear cut as this. In *H. hislopil* subsp. *robusta* the corolla tube is much less noticeably swollen in the base than usually occurs in subsp. *hislopil* and it is more or less unicoloured towards the base rather than distinctly transversely lined. The inner corona lobes are more robust than in subsp. *hislopil* and are slightly swollen at their apices.

In *H. longituba* subsp. *cashelensis* the base of the tube is slightly swollen and the inner corona lobes are thicker and much less obviously swollen at their tips than in subsp. *longituba*. In both these features it is rather more like subsp. *hislopil* than *H. longituba* subsp. *longituba*. The corolla is particularly variable in colour and shape. Inside it may have quite fine spots but these may also be very coarse and bold. It may also be relatively flat outside the mouth of the tube, as is often found in *H. hislopil* and is unknown in subsp. *longituba*. Finally, it should be noted that subsp. *cashelensis* occurs in quite close proximity to *H. hislopil* and is geographically very isolated from *H. longituba* subsp. *longituba* (cf. figs. 5.168 and 5.182). There is every reason to believe, therefore, that it is more closely allied to *H. hislopil* than to *H. longituba* and here it is transferred to *H. hislopil*.

The complications associated with *H. occulta* are mentioned below under that species.

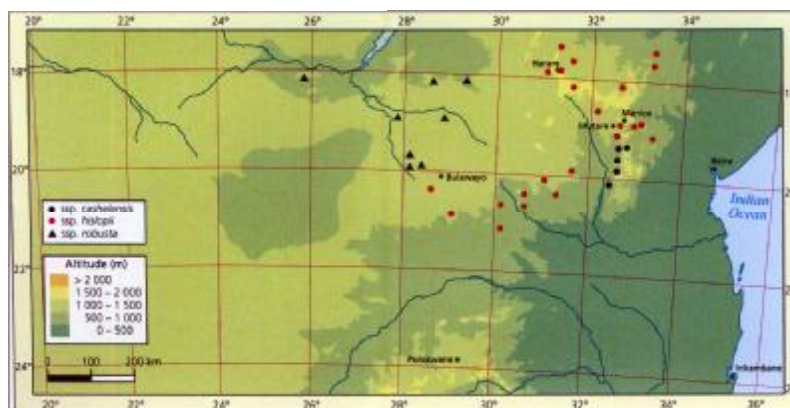


Fig. 5.168. Distribution of *Huernia hislopil*.

24a. *Huernia hislopiae* subsp. *hislopiae*

Stems 5-angled; tubercles united into low wings along stem. *Corolla* inside spotted and concentrically lined with maroon right to base, papillae with apical bristle much shorter than papilla; *tube* clearly swollen near base with upper portion $\pm$ equal in length to swollen part; *lobes* mostly longer than broad. *Inner corona lobes* not at all swollen at apex.

Distribution and habitat

Subsp. *hislopiae* has proved to be widespread in Zimbabwe, mainly in the south and in the east of the country. In the south it has been recorded from the Matopos near Bulawayo, eastwards to around Bikita and in the north-east from Harare towards Nyanga. It is also found in Moçambique, east of the Nyanga highlands in a relatively narrow band from Guro southwards to near Mt Zembe, south of Chimoio (Vila Pery).

Subsp. *hislopiae* is almost always found on gently sloping, granitic 'whalebacks' where it grows in patches of shallow soil in depressions in the granite among grasses, sometimes with *Myrothamnus flabellifolius* or with a mixture of low succulent shrubs of *Aloe*, *Euphorbia* and *Sarcostemma*. Plants are mainly found on the solid parts of these domes, rather than among patches of boulders.

Diagnostic features and relationships

Specimens of subsp. *hislopiae* form dense clumps of stems which are frequently 300-500 mm in diameter and may even be much larger.

Subsp. *hislopiae* has comparatively large flowers. In the centre there is a relatively short, steep-sided tube with a curious shape. It consists of two parts, an almost hemispherical

basal part which ends with a distinct thickening. This lower area is smooth and concentrically ringed with maroon on cream. Above this the tube becomes cylindrical and somewhat constricted before flaring at the mouth and it is densely and coarsely papillate, with maroon bars on cream. Beyond the mouth of the tube these papillae decrease rapidly in length, with much smaller ones covering the whole of the inside, including the lobes. This area is usually



Fig. 5.169. *H. hislopiae* subsp. *hislopiae*, PVB 7399, south of Chimoio, Manhica Province, Moçambique. A very large plant, growing on a low, granite dome among grasses and plants of *Euphorbia granitica*, with *H. leachii*, December 1997.

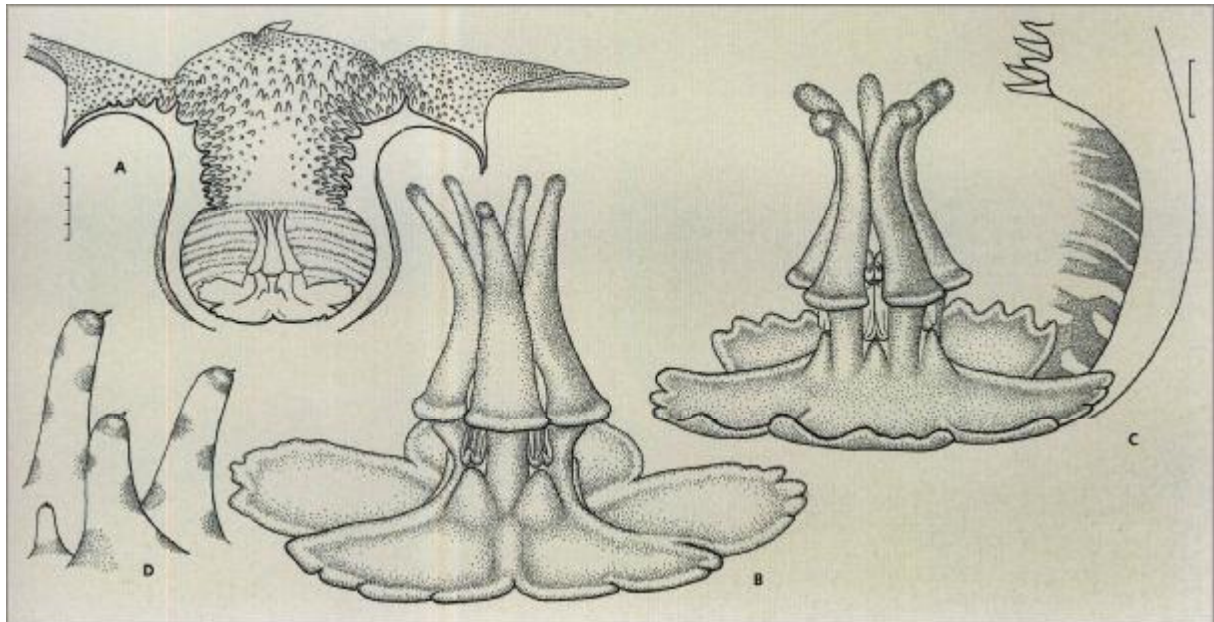


Fig. 5.170. *Huernia hislopiae* (A, B, D, subsp. *hislopiae*; C, subsp. *robusta*). A, side view of dissected flower. B, C, side view of gynostegium (in C with part of corolla tube). D, papillae inside corolla in mouth of tube. Scale bars: A, 5 mm; B, C, 1 mm (at C); D, 0.5 mm (at A). Drawn from A, B, PVB, near Zaka, Zimbabwe; C, PVB 7457, 30 km west of Kadoma, Zimbabwe; D, PVB 7397, near Guro, Manhica Province, Moçambique.

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finely to quite coarsely spotted with maroon on cream and is generally more or less flat, with the lobes spreading or slightly recurved beyond it.

As is often the case in such papillate flowers in *Huernia*, the papillae are usually slightly thicker perpendicular to the length of the flower. Most of them are spotted with maroon on cream like the surface of the corolla and each has a minute apical bristle. The corona is very conventional, with broad, dark (often nearly black) outer lobes spreading on the base of the tube and inner lobes rising up in the centre and ending in a slightly tuberculate, obtuse tip.

The position *vis-a-vis* *H. occulta* appears to be less clear cut than Leach (1988) made it out to be. While the stems of subsp. *hislopilii* are mostly much stouter than in *H. occulta*, when plants of *H. occulta* grow in the open their stems may also become stout. Some plants with the slender stems which have been considered to be characteristic of *H. occulta* produce flowers with a fairly short tube, with a broad, flat area beyond the mouth (also more or less characteristic of *H. occulta*) but with the concentric rings of maroon in the base of the tube and the relatively tall gynostegium of subsp. *hislopilii*.

In a similar manner, among plants of subsp. *cashelensis*, one finds specimens in which the flowers are decidedly flatter around the mouth of the tube, with longer and more attenu-

ated lobes than are normally found in subsp. *cashelensis* and with the larger, dark spots of subsp. *hislopilii*. However, the base of the tube is only very slightly swollen, the papillae in the tube have longer apical bristles than in subsp. *hislopilii* (Leach 1988) and the inner corona lobes have somewhat clavate apices so that these features usually distinguish this subspecies from subsp. *hislopilii*.

History

The first records of subsp. *hislopilii* were made by a Miss Gibbs and by J. Ffolliot-Darling. Miss Gibbs' plants came from the Matopos and flowered in Harry Bolus' garden in December 1906. Ffolliot-Darling's collection came from near Harare and plants from this gathering flowered in February 1906 in Cape Town. According to records in the Bolus Herbarium, N.E. Brown wanted to name it after Miss Gibbs and so it would appear that her collection was made slightly earlier. A further early collection was made by C.P. Piers in 1911. It was only somewhat later that Alexander Hislop sent material, some of which was communicated to Kew and described in 1922 by Turrill. Hislop (c. 1880-1945) was initially a gardener at Kew who later lived in several places in Africa, including Oudtshoorn (around 1902) and Nigeria around 1908 (Kew archives). He collected mainly in

Zimbabwe. His material of this species came from near Rusapi, where it was collected in 1917 and flowered at Kirstenbosch in April 1918.

After this, *H. hislopilii* seems to have suffered remarkably from being confused with other species, especially with *H. kirkii*. This confusion appears to have begun with the figure in *Flowering Plants of South Africa* (Phillips 1932a), which was taken as representing *H. kirkii* while in fact it was *H. hislopilii* subsp. *robusta*. All the figures of *H. kirkii* in White & Sloane (1937: fig. 1002-1005 and Plate 29) are of *H. hislopilii* subsp. *hislopilii* and the same is true of the upper figure on page 224 of Lückhoff (1952). Leach & Plowes (1966a) were the first to sort out this confusion.



Fig. 5.171. *H. hislopilii* subsp. *hislopilii*, 12 km south-west of Mutoko, Zimbabwe, in habitat, December 1997.



Fig. 5.172. *H. hislopilii* subsp. *hislopilii*, PVB 7759, near Guro, Manhica Province, Mocambique.

24b. *Huernia hislopiae* subsp. *robusta*

Huernia hislopiae subsp. *robusta* L.C. Leach & Plowes, J. S. African Bot. 32: 53 (1966).
Type: Zimbabwe, Lupani distr., Mabikwa, Leach 1628 (SRGH, holo.; BM, CAH, G, K, UISC, PRE, iso.).

Stems with 5 (-7) fairly prominent wing-like angles. Corolla inside only obscurely concentrically lined with maroon in basal portion of tube or wholly maroon there; papillae with apical bristle much shorter than papilla; tube slightly swollen near base with upper portion longer than swollen part; lobes mostly shorter than broad. Inner corona lobes slightly swollen at apex.

Distribution and habitat

Subsp. *robusta* is only found in the western part of Zimbabwe. It has been somewhat scantily recorded from the Hwange Game Reserve eastwards to near Kadoma (Gatooma) and southwards to near Bulawayo.

Subsp. *robusta* grows on sandy or gravelly flats among *Acacia* or *Colophospermum mopane*. Plants are often concealed under small shrubs.

Diagnostic features and relationships

Specimens of subsp. *robusta* rarely form clumps larger than 150 mm across and have relatively laxly spreading stems.



Fig. 5.173. *H. hislopiae* subsp. *robusta*, PVB 7457, 30 km west of Kadoma, Zimbabwe.

In subsp. *robusta* the corolla tube is not so noticeably swollen as in subsp. *hislopiae* and the swollen part occupies only a short distance near the base. Towards the base the inside of the tube is also less clearly marked with concentric maroon rings and it may even be wholly dark maroon. Beyond the tube, the corolla tends to be less flat than in subsp. *hislopiae* and it is often marked with broad, pinkish spots so that, overall, it has more of a pinkish hue than flowers of subsp. *hislopiae*.

This taxon then comes rather more close to *H. longituba*. From *H. longituba*, *H. hislopiae* is mainly distinguished by the lack of distinctly clavate tips to the inner corona lobes. However, the value of this distinction is uncertain since they may actually be slightly clavate in subsp. *robusta*.

History

This taxon was figured (as *H. kirkii*) in Phillips (1932a) from material reputedly collected by J.J. van Nouhuys near Barberton. The locality is almost certainly an error as it has never been seen in that relatively well-collected area again or, for that matter, anywhere inside South Africa. Documented material from the western part of Zimbabwe seems to have appeared for the first time around 1960.

24c. *Huernia hislopiae* subsp. *cashelensis*

Huernia hislopiae subsp. *cashelensis* (L.C. Leach & Plowes) Bruyns, comb. nov.
Huernia longituba subsp. *cashelensis* L.C. Leach & Plowes, J. S. African Bot. 32: 49 (1966).
Type: Zimbabwe, ± 10 km west of Cashel, Leach 5404 (PRE, holo.; K, SRGH, iso.).

Stems 5- (-6-) angled; tubercles united into low wings along stem. Corolla inside spotted and concentrically lined with maroon to near base; papillae with apical bristle up to as long as papilla; tube slightly swollen near base with upper portion longer than swollen part; lobes ± as long as broad. Inner corona lobes slightly swollen at apex.

Distribution and habitat

Subsp. *cashelensis* is found along the western flank of the Chimanimani Mountains from about 40 km south-east of Mutare southwards to near Chipinge and it has been recorded only on the eastern side of the Sabi River.

Plants usually grow on dry, fairly bare slopes in open *Brachystegia* woodland on gravelly soils derived from granite or dolerite.

Diagnostic features and relationships

Stems of this taxon are usually 5-angled and often quite short, forming small but quite dense clumps.

The flowers are tubular, with the relatively short corolla lobes erect to spreading around the mouth of the tube and the corolla tube slightly swollen at the base. The inside of the tube is cream with fine, red-brown spots which are somewhat concentrically arranged in the lower third of the tube, sometimes forming rings towards the base and with a solid, pentagonal, red-brown patch around the corona.

The somewhat shorter corolla lobes and more tubular corolla that is finely spotted with red-brown are all suggestive of *H. longituba*. However, as noted above, all these features are variable and, in one population recently seen, plants varied from ones typical of subsp. *cashelensis* to others where the flowers were



Fig. 5.174. *H. hislopiae* subsp. *cashelensis*, PVB 7415, near Cashel, Zimbabwe, a plant with a narrower corolla tube than in the next picture.

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very hard to separate from subsp. *hislopii*, though vegetatively they were indistinguishable from the others. The only more or less constant feature of this subspecies seems to lie in the shape of the papillae inside the corolla: each of them has an apical bristle which points towards the tips of the lobes and may be as long as the papilla itself.

This intergrading with subsp. *hislopii* suggests that this is where the affinities of subsp. *cashelensis* lie, rather than with the geographically very distant *H. longituba*, of which the nearest known population is nearly 1 000 km away. Consequently a new combination is made here so that this becomes the third subspecies of *H. hislopii*.

History

Subsp. *cashelensis* seems to have been collected for the first time by Leach in 1958 and further collections were made by D.C.H. Plowes and others after 1965.



Fig. 5.175. *H. hislopii* subsp. *cashelensis*, PVB 7415, near Cashel, Zimbabwe.

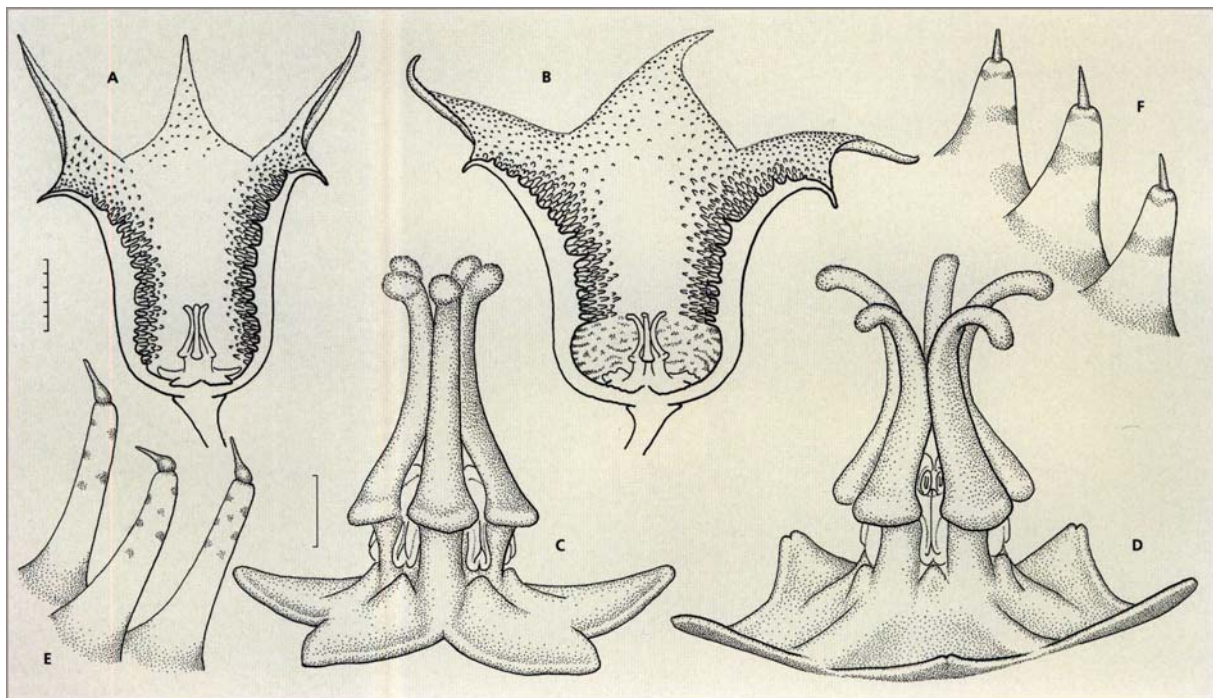


Fig. 5.176. *Huernia hislopii* subsp. *cashelensis*. A, B, side view of dissected flower. C, D, side view of gynostegium. E, F, papillae inside corolla in mouth of tube. Scale bars: A, B, 5 mm (at A); C, D, 1 mm (at C); E, F, 0.5 mm (at C). Drawn from PVB 7415, near Cashel, Zimbabwe.

25. *Huernia kirkii*

Huernia kirkii N.E.Br., R. Cap. 4 (1): 920 (1909).

Type: South Africa, Transvaal, Komatipoort, Kirk 76(K).

Huernia bicampanulata Verd., R. Pl. South Africa 12: t. 449 (1932).

Type: Transvaal, Naauport, Van Son sub PRE 10136 (PRE).

Succulent forming clump to 0.5 m diam. **Stems** 30-150 mm long, 8-12 mm thick (excluding teeth), decumbent to spreading, brownish or grey-green; **tubercles** 3-4 mm long, broadly deltoid, spreading, laterally flattened and joined into 5 slightly wing-like angles along stem, tapering abruptly to small acute tooth. **Inflorescence** of 1-5 flowers developing in gradual succession from short peduncle up to 5 mm long, with attenuate bracts 2-3 mm long; **pedicel** 6-25 mm long, 1.5 mm thick, spreading then ascending to hold flower facing upwards; **sepals** 6-10 mm long, 1.5-2.0 mm broad at base, narrowly ovate-acuminate. **Corolla** 20-30 mm long, 30-50 mm diam., bicampanulate; outside smooth, cream irregularly (sometimes very finely) spotted with pink, with 4-5 raised longitudinal veins running down each lobe onto tube; inside cream spotted with red or maroon changing to solid blackish maroon in tube, papillate all over except below thickening in tube, papillae reaching max. length of 2 mm and densest towards mouth of tube then decreasing in length gradually onto lobes, dark maroon tipped with short bristle; **tube** up to 20 mm long, at most slightly swollen in base, often pentagonal; **lobes** 8-10 mm long, 11-15 mm broad at base, erect to slightly spreading, deltate, acuminate. **Corona** $\pm$ 6 mm tall, 7.5 mm broad, without basal stipe; **outer lobes** spreading on base of tube and partly fused to it, divided into 5 broad $\pm$ truncate and emarginate lobes, dark maroon; **inner lobes** 4.0-4.5 mm long, cream spotted with pale maroon, with darker tips, adpressed to backs of anthers near bases then connivent-erect and becoming divergent above, below dorsiventrally flattened with inflated dorsal gibbosity at base, with distinctly swollen bristly apex.

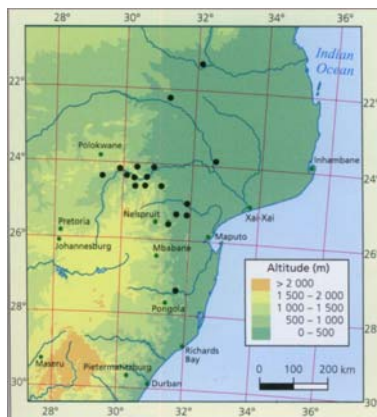


Fig. 5.177. Distribution of *Huernia kirkii*.



Fig. 5.178. *H. kirkii*, PVB 2034, Abel Erasmus Pass.

Distribution and habitat

Huernia kirkii is recorded from Mozambique and Zimbabwe as well as in Limpopo Province, Mpumalanga and KwaZulu-Natal of South Africa. In Zimbabwe it is found only in the south-eastern corner and the records from Mozambique are also all from localities which are adjacent to this area along the Limpopo River. In South Africa it is widely recorded from near Pietersburg (Polokwane) to Komatipoort and there is a single record in northern KwaZulu-Natal along the Pongola River.

Plants are usually found in flat areas in stony to sandy places under bushes or among trees. However, they have also been seen in mountainous places such as the lower to middle levels of the Abel Erasmus Pass and in shallow patches of soil on granite domes near Nelspruit.

Diagnostic features and relationships

Vegetatively *H. kirkii* cannot be distinguished very readily from *H. longituba*, though the stems are often more brightly mottled.

Flowers of *H. kirkii* are quite characteristically bicampanulate. The upper and wider bell is usually boldly and quite regularly spotted with maroon on cream inside but in the lower bell these spots coalesce near the mouth to solid dark maroon and the colour remains dark maroon to the base of the tube. In this area the papillae are also plain maroon and are not mottled. The base of the tube is hardly swollen at all and this inflation is not visible on the outside as it is in *H. hislopiae*, so from the

outside the lower part of the tube is more or less cylindrical.

In *H. kirkii* the inner corona lobes are quite long and they are noticeably swollen towards their tips.

History

Huernia kirkii was collected between 1900 and 1901 by John W.C. Kirk, a British soldier who was stationed for part of the Anglo-Boer War at Komatipoort.

Since its description, *H. kirkii* has been confused with *H. hislopiae* on many occasions. This seems, at least partly, to have been caused by a figure in the *Flowering Plants of South Africa* (Phillips 1932a) that appeared under the name *H. kirkii*. This figure is actually of *H. hislopiae* subsp. *robusta* and seems to have thrown White & Sloane (1937) completely off the scent of the 'real' *kirkii*, for all of their figures of *H. kirkii* are actually of *H. hislopiae* (mainly subsp. *hislopiae*). Similarly, the single figure which appeared under the name 'kirkii' in Lückhoff (1952) is also of *H. hislopiae* subsp. *hislopiae*.

HUERNIA LONGITUBA

26. *Huernia longituba*

Huernia longituba N.E.Br., H. Cap. 4 (1): 912 (1909).

Type: South Africa. Cape, Douglas, E. Pillans sub NS. Pillans 609 (BOL, holo.; GRA, iso.).

Small succulent forming clumps to 0.3 (-0.5) m diam. *Stems* 20-20 mm long, 10-20 mm thick (excluding teeth), decumbent, grey-green sometimes mottled with purple; *tubercles* 3-8 mm long, broadly deltoid, spreading, laterally flattened and joined into 4-5 fairly sharp angles along stem, tapering abruptly to small acute tooth. *Inflorescence* of 1-3 flowers developing in gradual succession from short peduncle, with attenuate bracts up to 6 mm long; *pedicel* 8-10 (-18) mm long, 2 mm thick, spreading to hold flower facing horizontally; *sepals* 8-10 mm long, 2 mm broad at base, narrowly ovate-acuminate. *Corolla* 20-28 mm long, 20-40 mm diam., tubular-campanulate; outside smooth, cream to pink with 3-5 raised longitudinal veins running down each lobe; inside cream finely spotted with red-brown or maroon becoming concentrically lined with red-brown or maroon in lower half of tube (below thickening), papillate except below thickening in tube, papillae reaching max. length of 1.5 mm and densest towards mouth of tube then decreasing in length gradually onto lobes, papillae cream spotted with maroon with apical bristle to 0.75 mm long; *tube* up to 20 mm long, only slightly expanded in basal half, gradually widening towards mouth, not pentagonal; *lobes* 8-10 mm long, 8-10 mm broad at base, erect to spreading, deltate, acuminate. *Corona* 5-6 mm tall, 8 mm broad, without basal stipe; *outer lobes* spreading on base of tube and partly fused to it, divided into 5 broad ± truncate and emarginate lobes, dark maroon; *inner lobes* 3-4 mm long, cream spotted with pale maroon, with darker tips, adpressed to backs of anthers near bases then connivent-erect and becoming divergent above, below dorsiventrally flattened with inflated dorsal gibbosity at base, with distinctly swollen bristly apex.

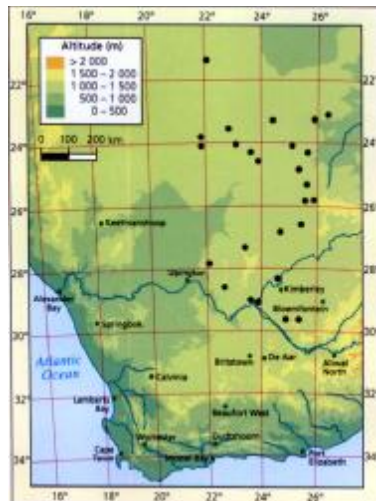


Fig. 5.182. Distribution of *Huernia longituba*.

Distribution and habitat

Huernia longituba is widespread in the southern half of Botswana, from north of Ghanzi to near Lobatse. In South Africa it is found from Kuruman and Mafikeng to Kimberley in the southern portion of the Kalahari as well as in the western part of the Free State between Lückhoff and Fauresmith, with a single record from further north near Delareyville.

In Botswana, plants are often found in sandy, flat areas under bushes or trees but further south they are mostly seen in stony, flat areas.



Fig. 5.179. *H. longituba*, PVB 2835, near Douglas.



Fig. 5.180. *H. longituba*, PVB 6444, west of Sekoma, Botswana.

Diagnostic features and relationships

Plants of *H. longituba* may form clumps up to 0.5 m in diameter and the stems are often quite loosely grouped, depending on the amount of shade received. The stems are more or less equally often 4-angled or 5-angled and the angles are usually quite sharp and clearly defined.

In *H. longituba* the flower generally has an almost cylindrical tube beyond which it is slightly flared, with the lobes almost erect to somewhat spreading. The inside is always finely spotted with maroon on a cream background and is densely papillate to just below the mouth of the tube, where the papillae suddenly disappear.

History

Huernia longituba was described from material collected in April 1906 by Eustace Pillans on the northern bank of the Orange River in Griqualand West near Douglas.



Fig. 5.181. *H. longituba*, PVB 6442, east of Sekoma, Botswana.



Fig. 5.183. *H. longituba*, 5 km south of Moshupa, Botswana, in habitat, December 1995.

27. *Huernia occulta*

Huernia occulta L.C. Leach & Plowes, J. S. African Bot. 32: 57 (1966).

Type: Zimbabwe, near Zimbabwe Ruins, Leach 11661 (SRGH, holo.; K, PRE, iso.).

Small succulent forming diffuse to very spreading clump 60-300 mm diam. (or more). Stems 30-150 mm long, 3-8 mm thick, decumbent to nearly prostrate when sheltered, grey-green; tubercles 2-4 mm long, deltoid, tapering abruptly into slender tooth 1.5-2.0 mm long, spreading, laterally slightly flattened and joined near base into (4-) 5 angles along stem. Inflorescence of 1 (-3) flowers developing in gradual succession on short peduncle (< 5 mm long), with slender lanceolate bracts 2-4 mm long; pedicel 8-20 (-25) mm long, spreading with upturned apex holding flower facing upwards; sepals 6-9 mm long, 1.5-2.0 mm broad at base, narrowly ovate-acuminate. Corolla 40-60 mm diam, bicampanulate with distinct saucer-shaped or shallowly bowl-shaped area below lobes and outside central tube; outside smooth, cream to pinkish sometimes very faintly pink-spotted, with 3-5 raised longitudinal veins running down each lobe onto tube; inside cream spotted with pale to dark brownish red changing abruptly to dark maroon in tube (becoming shiny around base), papillate all over except below thickening in tube, papillae reaching max. length of 1.25 mm and densest around mouth of tube then decreasing rapidly in length onto saucer- or bowl-shaped area, papillae maroon in tube becoming red-brown-tipped on cream on limb and lobes and with short apical bristle; tube 7.5-10 mm long, 7-10 mm broad at mouth, broadest and $\pm$ hemispherical towards base then

narrowing towards distinct thickening just below halfway up, remaining $\pm$ parallel-sided before widening abruptly at mouth, not pentagonal; lobes 10-12 mm long, 14-18 mm broad at base, erect to spreading or with recurved apices, deltate (longer than broad), acuminate to caudate. Corona 5.5-6.0 mm tall, 6-8 mm broad, without basal stipe; outer lobes spreading on base of tube and partly fused to it, divided into 5 broad $\pm$ truncate and emarginate lobes, dark maroon; inner lobes 3.5-5.0 mm long, dark maroon around base becoming cream, finely flecked with pale maroon for most of length, adpressed to backs of anthers near bases then connivent-erect and becoming divergent above, below dorsiventrally flattened with slightly downward-projecting dorsal gibbosity, tapering to small obtuse finely tuberculate apex.

Distribution and habitat

Huernia occulta is known only from the southern portion of Zimbabwe where it occurs in a belt between Bulawayo, Masvingo and Moodies Pass (some 80 km east of Masvingo) and up to about 100 km south of Masvingo.

This species is particularly associated with granitic domes or 'whalebacks' and seems to occur only on the solid outcrops, preferring low and more gently sloping large ones to the steeper and more precipitous mountains. Plants grow in dense, root-congested peat-like mats of shallow soil in island-like clumps of low vegetation on the solid slabs of granite. They are not found at all in the more bushy vegetation which develops among stones and boulders. Specimens usually grow

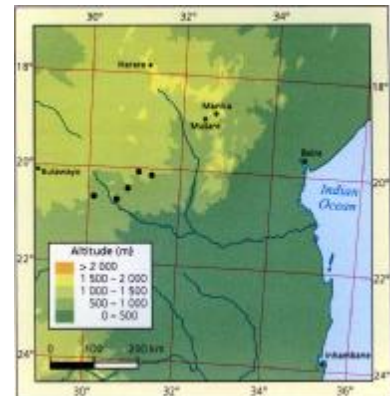


Fig. 5.184. Distribution of *Huernia occulta*.

inside patches of the sedge, *Coleochloa*, but they may even take shelter within clumps of *Myrothamnus flabellifolius*, *Sarcostemma viminale* or *Euphorbia griseola*.

Diagnostic features and relationships

Huernia occulta is usually immediately distinguishable by the slender stems (often only 3-5 mm thick) which, when well sheltered, become very long and nearly prostrate (as shown, for example, in White & Sloane 1937: fig. 1007). However, they actually vary quite

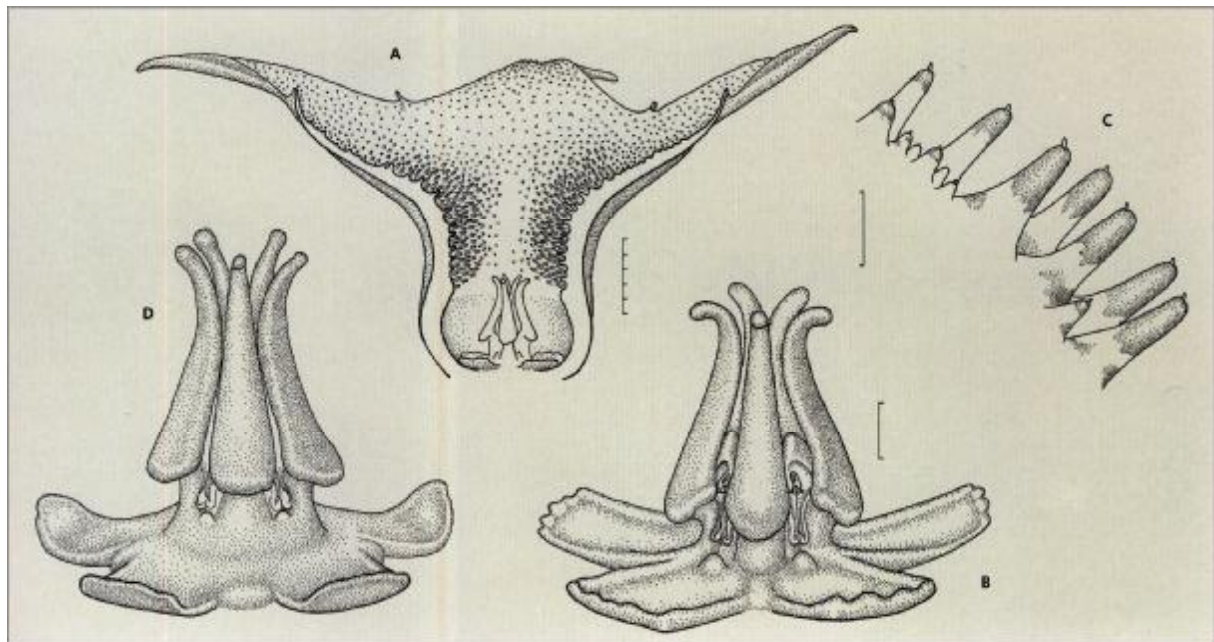


Fig. 5.185. *Huernia occulta*. A, side view of dissected flower. B, D, side view of gynostegium. C, papillae inside corolla in mouth of tube. Scale bars: A, 5 mm; B, D, 1 mm (at B); C, 0.5 mm. Drawn from A, C, D, PVB 7767, 60 km south of Masvingo, Zimbabwe; B, PVB 7461a, near Zaka, east of Masvingo, Zimbabwe.

HUERNIA OCCULTA

considerably, depending on the amount of shelter received, and they may be nearly erect and 6-8 mm thick if exposed (e.g. White & Sloane 1937: fig. 1006, see also fig. 5.186 here).

The flowers are distinctive both in shape and in colour. Generally they are bicampanulate, with a short, central, wholly dark maroon tube. This short central tube consists of a somewhat broader, smooth (i.e. not papillate), almost shiny lower part, above which there is a distinct thickening, where papillae suddenly appear. Above this it is cylindrical for a short distance and densely papillate. There is quite a lot of variation in the internal colouring of this tube and in some plants it has been found to be concentrically ringed in the base rather than solid maroon. Beyond the short central tube the corolla abruptly widens into a saucer-shaped to shallowly bowl-shaped structure which is spotted with brownish red on a cream background inside and finely papillate all over. The lobes are erect to spreading around this saucer-shaped part of the flower. They have the same colour as the saucer-shaped part of the corolla and when they spread out fully the flower has an impressive size (often 50 mm across or more) and is very striking.

While the dark maroon outer corona close to the base of the tube is not remarkable in any

way, the inner corona, which is paler than the outer, begins very close to the outer and has, in addition, somewhat decurrent basal swellings. Here the staminal tube is remarkably short for *Huernia* so that the anthers, too, are relatively close to the level of the outer corona.

Huernia occulta is often found in close proximity to the ubiquitous *H. hislopiae* subsp. *hislopiae* and also to *H. volkartii*. The latter has much smaller flowers with a different shape and cannot be confused with *H. occulta*.

The stems of *H. occulta* and *H. hislopiae* can usually be separated easily. Those of *H. occulta*, even when fairly stout and more or less erect, are much more weakly toothed with the teeth forming only slight wings along the stem (the teeth are larger and more clearly fused into angles along the stem in *H. hislopiae*). Thin-stemmed forms of *H. occulta* cannot be confused with *H. hislopiae* at all. Leach (1988) mentioned that the flowers can immediately be distinguished by the fact that the inside of the corolla tube is uniformly dark maroon in *H. occulta* and concentrically lined with maroon in *H. hislopiae*, but this is not always true. The corolla of *H. hislopiae* is generally flat to recurved outside the tube and this contrasts with its distinctively bicampanulate shape in *H. occulta*. The short staminal tube, with the inner

corona arising just above the level of the outer, is unique to *H. occulta* but reminiscent of the arrangement in such species as *H. urceolata*.

The shape and colouring of the inside of the flowers are very similar to those of *H. kirkii* but the stems and the inner corona of *H. occulta* make separation fairly easy from *H. kirkii*.

History

Huernia occulta was first collected, it seems, by Georges van Son during the Vernays-Lang Kalahari Expedition of 1930, when plants were gathered near the Zimbabwe Ruins in the Masvingo district. These plants were considered to represent *H. hislopiae* and were figured by White & Sloane (1937: fig. 1006-1008) under that name. This material was also illustrated in *Flowering Plants of South Africa* (Phillips 1939) under the name *H. hislopiae*. Lückhoff seems to have been aware of it (since fig. 1007 of White & Sloane (1937) was taken by him) but he left it out of his book. Leach & Plowes (1966a) were the first to realise that these collections constituted a species distinct from *H. hislopiae* and described it from material collected by Leach near the Zimbabwe Ruins just before or during 1958.



Fig. 5.186. *H. occulta*, PVB 7767, 60 km south of Masvingo, Zimbabwe, showing the range of thickness of the stems in this population.



Fig. 5.187. *H. occulta*, PVB 7767, 60 km south of Masvingo, Zimbabwe, this and the next picture give an impression of the variability of the flowers in one locality.



Fig. 5.188. *H. occulta*, PVB 7767, 60 km south of Masvingo, Zimbabwe.



Fig. 5.189. *H. occulta*, PVB 7461a, near Zaka, east of Masvingo, Zimbabwe. Here the flower does not have the typically dark corolla tube but the corona is the usual one.



Fig. 5.190. *H. occulta*, PVB 7462, east of Bikita, Zimbabwe.

28. *Huernia levyi*

Huernia levyi Obermeyer, *Fl. Pl. South Africa* 16: t. 616 (1936).

Type: Zimbabwe, Hwange, Levy sub Herb. Transvaal Mus. 3:142 (PRE).

Small succulent forming loose clump 80-300 mm diam. *Stems* 40-100 mm long, 8-15 mm thick, decumbent, dull green to purplish with faint darker mottling; *tubercles* 4-10 mm long, deltoid, spreading, laterally much flattened and joined into 4-5 wing-like angles along stem, slightly flattened on upper surface, tipped by slightly swollen leaf-rudiment. *Inflorescence* of 1-3 flowers developing in gradual succession from lower half of stem on short peduncle (up to 5 mm long) with few narrowly attenuate bracts 2-3 mm long; *pedicel* 7-11 mm long, 1 mm thick, spreading and descending with flower then ascending from this position, pinkish; *sepals* 5-6 mm long, 1.5-2.0 mm broad at base, ovate-acuminate. *Corolla* 25-40 mm long, 20-25 mm diam., tubular-campanulate; outside papillate, pink mottled with cream towards mouth, with 3-5 raised longitudinal veins running down from apex of each lobe; inside dark maroon in lower half changing to maroon spots on cream above, papillate all over except below annular thickening near base of tube, papillae short and dense on this thickening, reaching max. length of 1.00-1.25 mm a little above it then decreasing in length gradually onto lobes, each with apical bristle reaching max. length of 2 mm where papillae longest and rapidly decreasing in length above and below this; tube 22-35 mm long (occupying most of flower), widening gradually towards mouth, not pentagonal, with distinct annular thickening 3-5 mm above base; *lobes* 5-8 mm long, 12-15 mm broad at base, somewhat spreading, deltate, shortly acuminate. *Corona* 4-5 mm tall, 5 mm broad, without basal stipe; *outer lobes* spreading on base of tube and partly fused to it, indistinct and fused into disc, dark maroon; *inner lobes* 3.0-3.5 mm long, red to brownish becoming darker towards tips, adpressed to backs of anthers at base then connivent-erect, below dorsiventrally flattened with inflated dorsal gibbosity at base, above stout and almost terete, obtuse and somewhat clavate, finely tuberculate at apex.

Distribution and habitat

Huernia levyi is mainly found along the Zambezi Valley. Collections have been made in the eastern corner of the Caprivi Strip of Namibia on Impalila Island, along the north-eastern border of Botswana to as far south as Pandamatenga.



Fig. 5.191. *H. levyi*, PVB 6958, north of Pandamatenga, Botswana.

HUERNIA LEVYI

In Zambia, apart from records from around Livingstone and along Lake Kariba, it is found in locally dry areas as far north as Monza. The species is best known in western Zimbabwe, where it is recorded from Kariba and Hwange southwards to Gokwe.

Plants generally occur in stony places in relatively low-lying, hot areas among small bushes and often between trees of *Colophospermum mopane*.

Diagnostic features and relationships

The stems of *H. levyi* form loose, slightly spreading clumps. They have more deeply and sharply winged angles than in *H. hislopilii* or *H. longituba*, though in this respect they are somewhat similar to those of *H. hislopilii* subsp. *robusta*.

The flower of *H. levyi*, which may reach a length of 40 mm, is the longest known in *Huernia*. It consists mainly of a long tube, with short lobes hardly spreading at all around the mouth. The outside is noticeably rough with papillae and is mostly a dull pink. The tube gradually widens from the base to a somewhat flared mouth. Inside, it is uniformly dark maroon near the base, becoming maroon spotted with cream towards the mouth. A little above the base there is a thickened ring of tissue (an 'annulus') which projects somewhat from the sides of the tube. Below this ring, the interior of the flower is smooth, i.e. without papillae. Papillae begin to appear on the 'annulus' but here they are small and particularly densely clustered. Above it they increase greatly in length and each is also tipped by a fairly long

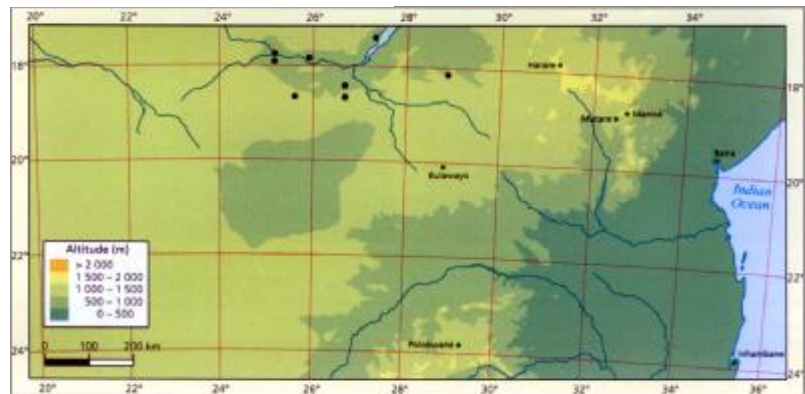


Fig. 5.192. Distribution of *Huernia levyi* in southern Africa.



Fig. 5.193. *H. levyi*, PVB 9584, among mopane bushes near Sinazongwe, Zambia, December 2003.

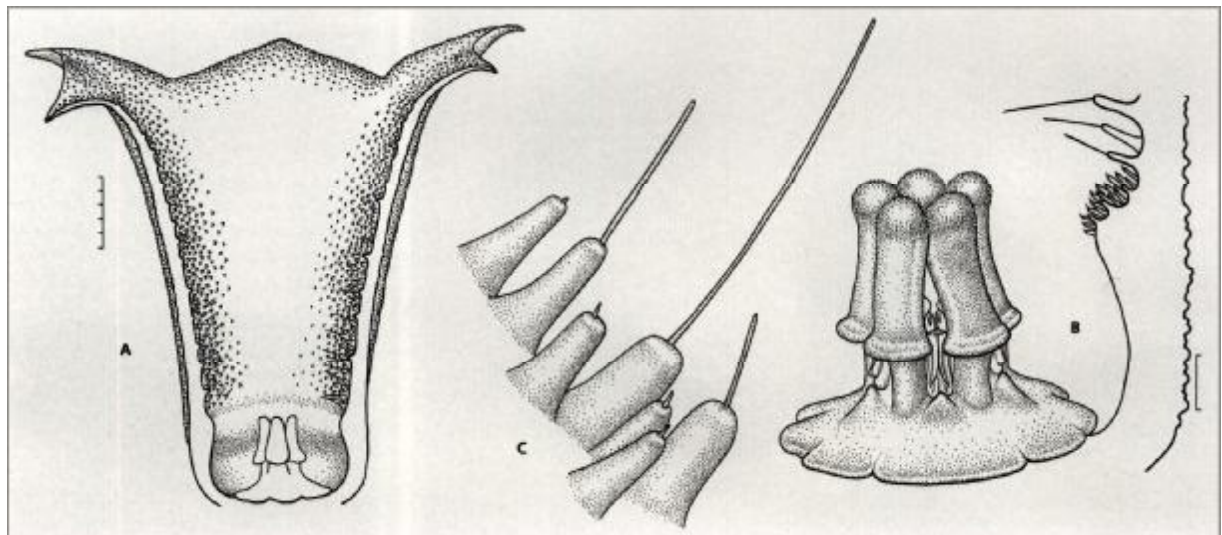


Fig. 5.194. *Huernia levyi*. A, side view of dissected flower. B, side view of gynostegium and part of centre of corolla. C, papillae inside corolla just above small 'annulus'. Scale bars: A, 5 mm; B, 1 mm; C, 0.5 mm (at A). Drawn from PVB 6958, north of Pandamatenga, Botswana.



Fig. 5.195 *H. levyi*, PVB 6958, north of Pandamatenga, Botswana. The noticeably papillate exterior of the corolla can be seen here.

bristle, which may exceed the length of the papilla itself. They gradually decrease in length again towards the mouth of the tube, with the apical bristle disappearing more rapidly.

The outer corona forms a more or less continuous dark maroon disc adpressed to the base of the tube, with the lobes only recognisable as indentations around its perimeter. The inner lobes are more unusual. They are relatively long and almost erect and they change from dorsiventrally flattened near the base to thick and more or less clavate at the rounded, fairly bristly tips.

It would appear that *H. levyi* and *H. hislopilii* subsp. *robusta* are most closely related (differing by the longer flower in *H. levyi* and the longer and apically less swollen inner corona lobes in subsp. *robusta*) and that both occur in the area between Hwange and Gokwe. Variation in *H. levyi* has, so far, been little documented and it is unclear whether the two maintain their distinctness.

History

According to records in the Bolus Herbarium this species was first gathered by Sidney Tapscott in February 1928 in Zambia near Broken Hill. The material collected by B. Levy in about 1932 near Hwange in Zimbabwe was described in 1936 by Obermeyer as *H. levyi*. Around this time several collections were made by Frederick Eyles, also near Hwange and by the land surveyor Frank W. Porter in the Mazabuka district of southern Zambia.

Benjamin Levy (May or June 1896-?) was a pharmaceutical chemist by profession. A Jewish Englishman, he was born in Connecticut in the United States and worked from about 1928 till at least 1952 in Zimbabwe, most of the time as an assayer at the Wankie Colliery Company in Hwange.

Key to the varieties of <i>H. volkartii</i>	
Stems decumbent	
to erect	29a. var. <i>volkartii</i>
Stems prostrate	29b. var. <i>repens</i>

29. *Huernia volkartii*

Huernia volkartii Peitsch. ex Werderm. & Peitsch., *Gartenflora* 85: 78 (1936).

Type: Angola, Cuanza Sul distr., Vila Nova de Seles, Gossweiler (missing).

Neotype (selected here): A.C. White & B. Sloane, *Stap.*, ed. 2, 3: fig. 958.

Small succulent forming clumps or mats up to 1 m diam. Stems 25-300 (-500) mm long, 5-8 mm thick (excluding teeth), decumbent to erect, grey-green to reddish; tubercles 2-3 mm long, spreading, deltoid, slightly laterally flattened and joined in (4-) 5 angles along stem, narrowing abruptly into small slightly subulate tooth. Inflorescences 1 per stem near base, of 1-3 flowers developing in gradual succession from short peduncle with slender filiform bracts 3-4 mm long; pedicel 6-12 mm long, 1 mm thick, spreading with ascending apex holding flower facing slightly upwards; sepals 5-8 mm long, 1 mm broad at base, narrowly attenuate. Corolla 20-30 mm diam., campanulate; outside papillate, cream suffused with maroon to brown, with 5 raised longitudinal veins running down lobe and onto tube; inside cream with irregular ± concentric maroon rings in tube becoming irregular blotches on lobes, densely covered with somewhat radially compressed papillae from halfway down tube onto lobes, papillae up to 2.5 mm long in mouth of tube and rapidly decreasing in length on lobes, cream ringed or spotted with maroon and sometimes with minute apical bristle; tube 6-9 mm long, 10-15 mm broad at mouth, cupular, not pentagonal, slightly thickened just above middle (where papillae end); lobes 4.5-9.0 mm long, 7.0-9.5 mm broad at base, spreading to recurved, deltate, acuminate, flat with margins slightly folded up especially towards tip. Corona 3.5-6 mm tall, 5-6 mm broad, without basal stipe; outer lobes 1-2 mm long, often rectangular and apically bifid, spreading on base of tube, dark maroon; inner lobes 2.5-4.0 mm long, cream flecked with dark maroon becoming maroon towards base, adpressed to backs of anthers then rising up connivent and diverging towards apices, tapering gradually from broad dorsal gibbosity then swelling again to thickened and sometimes horizontally spreading finely tuberculate truncate apex.

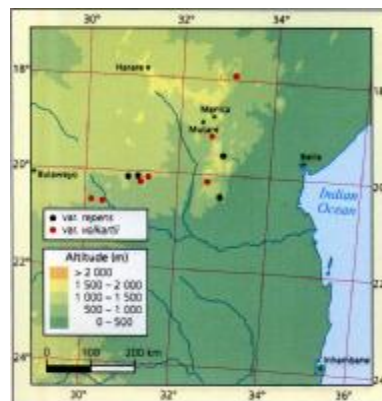


Fig. 5.196. Distribution of *Huernia volkartii* in southern Africa.

29a. *Huernia volkartii* var. *volkartii*

Huernia volkartii Gossweiler in A.C. White & B. Sloane, *Stap.*, ed. 2, 3: 907 (1937).

Type: Angola, Cuanza Sul distr., Vila Nova de Seles, Gossweiler (missing).

Lectotype (selected here): A.C. White & B. Sloane, *Stap.*, ed. 2, 3: fig. 958.

Huernia montana Kers, *Bot. Notis.* 122:179 (1969). Type: Angola, Chela Mountains, Kers 3460 (S).

Stems decumbent to erect, 25-50 (-80) mm long.

Distribution and habitat

Huernia volkartii var. *volkartii* has a most unusual distribution. It is known in Angola from the Chela Mountains in the south at least as far north as between Gabela and Quibala in the central Cuanza Sul district. It is also found in the south of Zimbabwe and in the east along the Chimanimani and Nyanga Mountains where it extends on outliers of these mountains (such as the Choa Mountains) into Mozambique. The areas in Angola and Zimbabwe where it occurs are separated by roughly 1 800 km.

In Zimbabwe and Mozambique var. *volkartii* generally grows at relatively high altitudes of 1 000-1 550 m on granite mountains. Here plants are found occasionally among *Myrothamnus flabellifolius* (the resurrection bush) and *Selaginella* in patches of shallow soil on exposed rock. More frequently, plants grow in accumulations of loose leaf-litter and shallow soil that cover rock slabs in the patches of low *Brachystegia* forest that can develop on certain rocky slopes or between the most exposed places on granite domes. It appears that the habitat in Angola is similar (Leach 1988).

Diagnostic features and relationships

The stems of var. *volkartii* usually seem to be decumbent with only the upper half almost erect or they may be practically prostrate. They are generally more slender than those of the frequently sympatric *H. hislopilii* and shorter, squatter and more densely clustered than those of *H. occulta*, with which it also occurs in the Masvingo area of Zimbabwe.



Fig. 5.197. *H. volkartii* var. *volkartii*, PVB 7460, south of Mberengwa, Zimbabwe, with slightly shorter corolla lobes.

HUERNIA VOLKARTII

In *H. volkartii* the flowers are relatively small but are prettily marked inside with maroon on cream. The outside of the corolla is papillate and this is the case inside too, where there are prominent papillae above the thickening in the tube, which become progressively smaller on the lobes. They emit a fairly strong, excrement-like odour. The corona has dark maroon outer lobes and much paler inner ones which have a thick, swollen, truncate apex.

Huernia volkartii is very similar to *H. stapelioides* and is most easily separated by its

predominantly 5-angled stems which are far smaller and more slender than those of *H. stapelioides*. Leach (1988) mentioned other minor differences such as the shorter, less tapering corolla lobes and more obtuse, less papillate inner corona lobes.

Huernia volkartii, *H. loeseneriana* and *H. stapelioides* are very closely related indeed and might easily be taken as belonging to a single widespread species, as implied by Plowes (1971: 16). In *H. volkartii* the stems are almost always 5-angled while in the other two they are nearly

always 4-angled. In *H. loeseneriana* the corolla lobes are about as long as broad while in *H. stapelioides* they are noticeably longer than broad. In *H. volkartii* the position is somewhat equivocal as they are mostly as broad as long but may also be longer. The papillae inside the corolla are shorter in *H. loeseneriana* than in either of the others, reaching a maximum length of 1.5 mm, while regularly exceeding 2 mm in the other two species.

It is not clear whether the Angolan material of *H. volkartii* is identical to that called *H. volkartii* from Zimbabwe. Material from Zimbabwe seems to have been associated first with *H. volkartii* by Plowes (1971). The material of Gossweiler's which was figured in White & Sloane (1937) has a very different appearance, with narrow, dark, very weakly angled stems, though it appears that the flowers are similar.

History

Huernia volkartii was first collected by John Gossweiler sometime before 1935 at Vila Nova de Seles in central Angola. He published a description of this collection in White & Sloane (1937) but seems to have sent material to Germany and the name was first used in 1936 for this material by Alfred Peitscher and was validly published in 1936 by Werdermann and Peitscher. Gossweiler named it after a friend, George Volkart of Wintertur, in Switzerland. It seems that L.C. Leach first recorded *H. volkartii* in Zimbabwe, with a collection from east of Masvingo which flowered in cultivation in 1957 (Leach 1976a).



Fig. 5.198. *H. volkartii* var. *volkartii*, PVB 7460, south of Mberengwa, Zimbabwe.

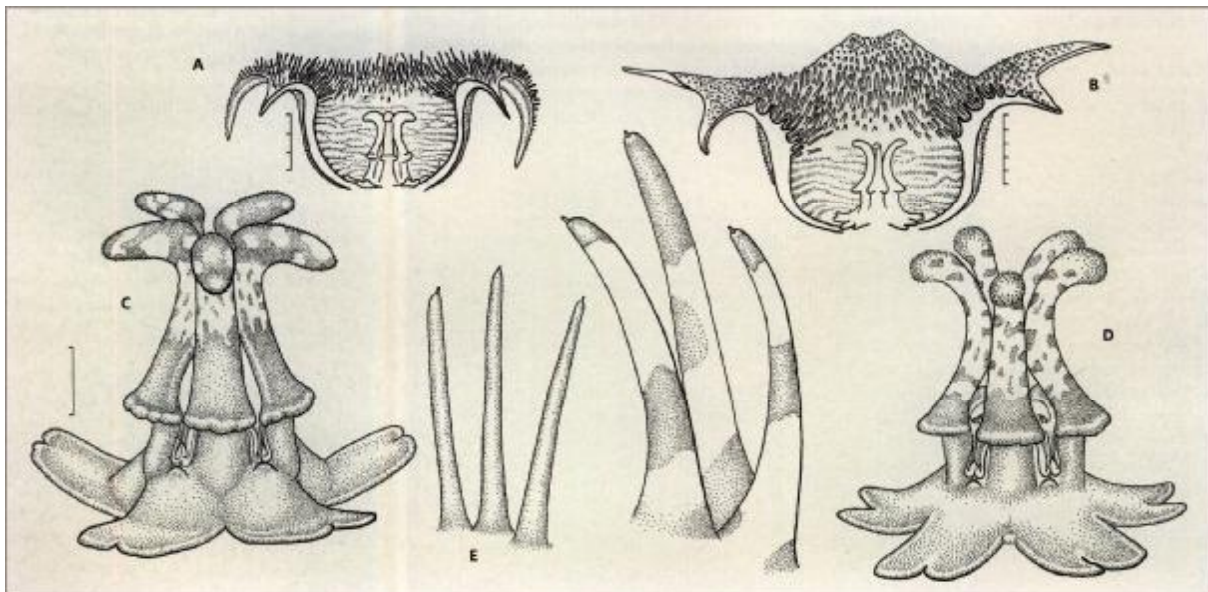


Fig. 5.199. *Huernia volkartii* (A, C, E, var. *repens*; B, D, F, var. *volkartii*). A, B, side view of dissected flower. C, D, side view of gynostegium. E, F, papillae inside corolla in mouth of tube. Scale bars: A, 3 mm; B, 5 mm; C, D, 1 mm (at C); E, F, 0.5 mm (at C). Drawn from A, C, E, PVB 7408, east of Espungabera, Manhica Province, Mocambique; B, D, F, PVB 7460, south of Mberengwa, Zimbabwe.

29b. *Huernia volkartii* var. *repens*

Huernia volkartii var. *repens* (Lavranos) Lavranos, J. S. African Bot. 38: 43 (1972).

Huernia repens Lavranos, J. S. African Bot. 27:11 (1961).

Type: Moçambique, Manica e Sofala, 'Jaegerslust' near Garuso, Schweickerdt 3469 (PRE, holo.; SRGH, iso.).

Stems prostrate, 25-300 (-500) mm long.

In parts of the Masvingo district of southern Zimbabwe and in Moçambique adjacent to the Chimanimani Mountains, plants of *H. volkartii* may have long, wholly prostrate stems which can reach lengths of up to 0.5 m or more. Plants of var. *repens*, as these are known, typically form dense mats in leaf-litter on the floor of forests or may dangle from cliffs in shaded areas.

In var. *repens* the angles are usually rounded and the teeth on the tubercles are more or less obsolete. These plants were initially recognised as a separate species, *Huernia repens*. Once the existence of *H. volkartii* in Zimbabwe had been established and it was realised how similar the flowers of *H. repens* were to those of *H. volkartii*, Leach seems to have advised that *H. repens* ought to be given varietal status under *H. volkartii* (Lavranos 1972).

Leach (1988) included a collection from the Choa Mountains north-west of Catandica under var. *repens*. My own collection from there has shown these plants to be more similar to var. *volkartii* and they are included under var. *volkartii* on the distribution map.

Material of var. *repens* seems to have been collected for the first time by H.G. W. Schweickerdt near Garuso in Moçambique in 1958.

30. *Huernia stapelioides*

Huernia stapelioides Schltr., Bot. Jahrb. Syst. 20, Beibl. 5:55(1895).

Type: South Africa, Transvaal, Nazareth, between Houtbosberg and Klipdam, 4500', Schlechter 4487 (B, destroyed).

Lectotype (selected here): A.C. White & B. Sloane, Stap., ed. 2, 3: fig. 948.

Huernia vogtsii E. Phillips, Fl. Pl. South Africa 12: t. 452 (1932).

Type: Transvaal, Crocodile Poort, Magaliesberg, Vogts sub PRE 1044 (PRE).

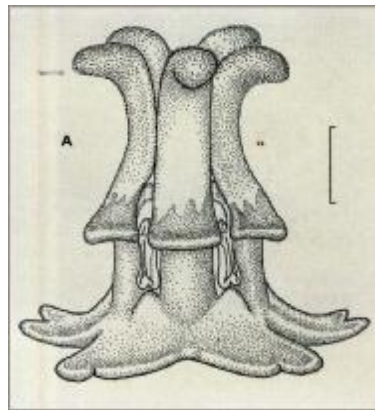


Fig. 5.201. *Huernia stapelioides*. A, side view of gynostegium. Scale bar: A, 1 mm. Drawn from hort. Aslander.



Fig. 5.200. *H. volkartii* var. *repens*, PVB 7408, east of Espungabera, Manhica Province, Mocambique.

Small succulent forming clumps of loosely packed stems up to 0.5 m diam. Stems 15-80 mm long, 10-15 mm thick, erect to spreading; tubercles laterally somewhat flattened and joined into 4 (-5) obscure to wing-like angles along stem. Inflorescence of 1-5 flowers developing in gradual succession, arising in lower half of stem from small peduncle with slender acuminate bracts 2-6 mm long without lateral teeth; pedicel 8-12 (-18) mm long, 1.0-1.5 mm broad at base, spreading and holding flower facing horizontally or slightly downwards; sepals 8-10 mm long, narrowly ovate-acuminate. Corolla 30-42 mm diam., campanulate; outside finely papillate, pale pink to brownish, with 3-5 raised longitudinal veins running down each lobe; inside cream with brown to maroon concentric broken lines becoming denser towards base of tube and solid brown to red around corona, with mottled papillae up to 2.5 mm long with minute apical bristle; tube $\pm$ 1.5 times as broad as long, cupular; lobes $\pm$ 1.5 times as long as broad, spreading with apices often recurved, deltate, slenderly acuminate. Corona 4-6 mm tall, 3-5 mm broad, without basal stipe; outer lobes $\pm$ 1 mm long, subquadrate to notched at apex, dark maroon; inner lobes 2.5-3.0 mm long, shiny maroon spotted with cream around base, becoming maroon above, adpressed to backs of anthers for their lower half, somewhat dorsiventrally flattened and broadened into transversely gibbous base, linear, above connivent-erect to slightly diverging into bristly and swollen to inverted foot-shaped apex.

Distribution and habitat

Huernia stapelioides is found in South Africa from north of the Soutpansberg to near Pretoria and eastwards to Burgersfort and Groblersdal along the edge of the escarpment. There are also a few records from Swaziland along the western foot of the Lebombo Mountains south of Stegi (Siteki).

Plants are generally found in flat areas, where they often grow under trees, but they have been located sometimes in rocky terrain.

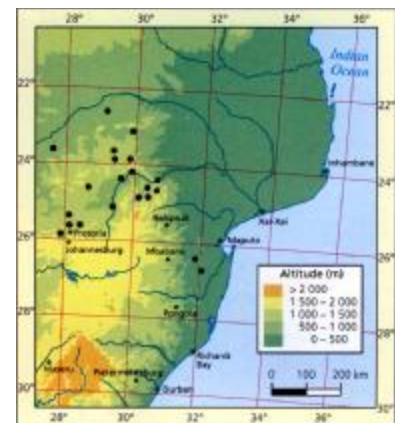


Fig. 5.202. Distribution of *Huernia stapelioides*.

HUERNIA LOESENERIANA

Diagnostic features and relationships

In *H. stapelioides* the stems often have a spreading and loosely mat-forming habit. They are more or less always 4-angled but vary very much in length depending on the amount of shelter received.

The inside of the flowers here is concentrically marked with maroon on cream, though very occasionally the dark markings are absent and the corolla is uniformly pinkish. As the lobes generally tend to fold back somewhat the flowers appear smaller than their actual diameter. The inside is covered with quite large papillae which extend to just inside the mouth of the tube and give the flower a very rough look.

In *H. stapelioides* the apices of the inner corona lobes are very variable in shape, from inverted foot-like as in *H. hystrix* to more or less spherically swollen. They are always noticeably bristly around their tips.

On account of the reflexed corolla lobes and particularly bristly corolla, *H. stapelioides* seems to have been confused with *H. hystrix* on occasion but, as Leach (1976a) and Kirsten (in White & Sloane 1937:903) made clear, the stems alone are sufficient to distinguish them. These two species actually grow together in several places in the area between the Soutpansberg and the Olifants River along the north-eastern escarpment. Though they are undoubtedly closely related, a closer relationship exists between *H. stapelioides* and *H. loeseneriana* and the differences between them are discussed under that species.



Fig. 5.204. *H. stapelioides*, De Kock 1327, Lekhlabile, near Nelspruit.



Fig. 5.203. *H. stapelioides*, PVB 1972, Derdepoort, Pretoria, an unusual, pale-flowered plant discovered by Emden Pienaar jr.

History

Huernia stapelioides was discovered by Rudolf Schlechter on 13 February 1894 growing in sand at Nazareth between Klipdam and Houtbosberg, in the Pietersburg (Polokwane) district.

Huernia vogtsii was described from material collected just north-west of Pretoria. It should perhaps be noted that fig. 949 in White & Sloane (1937), of a plant of '*H. vogtsii*' with 5-angled stems actually represents a plant of *H. nouhuysii*. As Leach (1976a) emphasised, 5-angled stems are particularly rare in *H. stapelioides*.

31. *Huernia loeseneriana*

Huernia loeseneriana Schltr., Bot. Jahrb. Syst. 20, Beibl. 5: 55 (1895).

Type: South Africa, Transvaal, rocks near Olifants R. 5000', Schlechter 3774 (B. destroyed).

Neotype: Transvaal, Olifants R., near Middleburg, Rossouw 92 (NBG).

Small succulent forming dense mats of tightly packed stems up to 1 m diam. Stems 15-60 (-80) mm long, 10-15 mm thick, erect, grey-green to brown; tubercles 3-5 mm long, spreading, deltoid, laterally flattened towards base and joined into 4 (-5) wing-like angles along stem, tapering into acute (when young) slightly darker tooth. Inflorescence of 1-5 flowers developing in gradual succession, arising in lower half of stem from small peduncle with slender acuminate bracts 2-6 mm long without lateral teeth; pedicel 3-10 mm long, 1.0-1.5 mm thick, spreading and holding flower facing horizontally or slightly downwards; sepals 6-8 mm long, narrowly ovate-acuminate. Corolla 18-26 mm diam., campanulate; outside finely papillate, pale pink to brownish, with 3-5 raised longitudinal veins running down each lobe; inside cream with brown to maroon concentric broken lines becoming denser towards base of tube and solid brown to red around corona, with obtuse conical dorsiventrally flattened papillae from just below middle of tube to mouth and onto lobes (max. length of ± 1 mm at mouth of tube), each with small apical bristle; tube 7-9 mm long, 7-10 mm broad at mouth, cylindrical, cupular, slightly broader than long; lobes 5-8 mm long, 6.5-9.0 mm broad at base, spreading with apices often recurved, deltate, acute. Corona 3.5-4.0 mm tall, 3-5 mm broad, without basal stipe; outer lobes ± 1 mm long, subquadrate to notched at apex, dark maroon; inner lobes 1.5-2.0 mm long, shiny maroon spotted with cream around base, becoming maroon above, adpressed to backs of anthers for their lower half, somewhat dorsiventrally flattened and broadened into transversely gibbous base, linear, above connivent-erect to slightly diverging at obtuse slightly swollen and bristly apex.

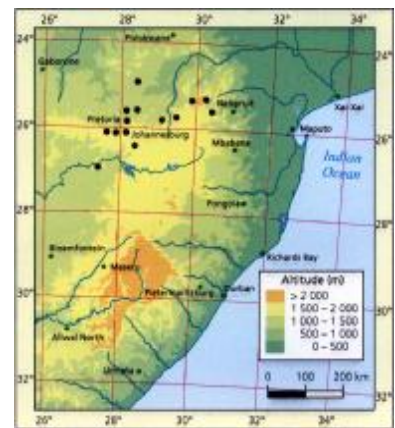


Fig. 5.205. Distribution of *Huernia loeseneriana*.

Distribution and habitat

Huernia loeseneriana is common on the summits of many of the hills and ridges of the Magaliesberg and the Witwatersrand around Pretoria and Johannesburg. From there it occurs southwards into the Free State around Parys as well as eastwards to Dullstroom and Waterval Boven on the edge of the escarpment near Lydenburg.

Plants are often found on sandstones but also occur on dolomite (e.g. south of Pretoria around Irene) and even on dolerite outcrops near Roossenekal. They always grow in stony, usually very exposed situations, often in pockets of shallow soil on exposed slabs of rock or tightly wedged into crevices between rocks.

Diagnostic features and relationships

Specimens of *H. loeseneriana* form dense mats, quite often up to 0.5 m in diameter and even larger on occasion. In these clumps the 4-angled stems are mostly very short (averaging 15-25 mm tall) and are packed extremely tightly.

The flowers are small and quite inconspicuous, with a slightly nodding habit. This often keeps them among the stems so that they are somewhat hidden, partially constricted by the surrounding stems and are unable to open fully. When the flowers are able to open properly, they consist of a short, cupular tube with the lobes spreading from its mouth. Their rather unattractive, pinkish exterior belies the striking markings on the inside. These are usually narrow, broken maroon lines on cream which become concentric lines on the tube and solid red around the corona. The flower emits a faint



Fig. 5.206. *H. loeseneriana*, PVB 6621, near Groblersdal.

odour of excrement. The inside of the tube is covered with papillae from halfway up the tube (where they are longest) and they then become much smaller on the lobes.

The corona has the usual dark maroon outer lobes adpressed to the base of the corolla tube and somewhat paler inner lobes which end abruptly in bristly, rather swollen apices.

Huernia loeseneriana is probably closest to *H. stapelioides*, which grows at lower altitudes in flat areas. In *H. stapelioides* the corolla lobes are considerably longer than broad, whereas they are about as wide as long in *H. loeseneriana* and this makes the flower somewhat larger in *H. stapelioides*. Furthermore, the papillae inside the flower are longer in *H. stapelioides* than in *H. loeseneriana*. The inner corona usually has a much more elaborate, foot-shaped apex in *H. stapelioides*, though this has been found to be variable (Leach 1976a; 1988).

History

Huernia loeseneriana was discovered by Rudolf Schlechter on 20 November 1893 and named by him in honour of the botanist L.E.T. Loesener of Berlin.



Fig. 5.207. *H. loeseneriana*, on the grounds of Pretoria University, Pretoria, growing on sandstone outcrops with *Euphorbia schinzii*, September 1979.

32. *Huernia whitesloaneana*

Huernia whitesloaneana Nel, Cact. Succ. J. (US) 8: 9 (1936).

Type: South Africa, Transvaal, Soutpansberg, Nel sub STE 5720 (NBG).

Dwarf succulent forming low dense mats. Stems 10-20 (-30) mm long, 5-8 mm thick (excluding teeth), erect, purplish green; tubercles 2-3 mm long, deltoid, spreading, laterally flattened towards base and there joined into 4-5 angles along stem, abruptly narrowing into acute tooth slightly flattened above. Inflorescence with 1-5 flowers developing successively from short peduncle; pedicel 4-8 mm long, $\pm$ 1 mm thick, spreading with ascending apex holding flower facing upwards; sepals 3-7 mm long, 1 mm broad at base, ovate-acuminate, recurved towards apices. Corolla 10-15 mm long, 12-22 mm diam., campanulate to cylindrical; outside smooth with 3-5 heavy paler raised longitudinal veins on lobes and upper parts of tube, purple-red mottled on cream; inside cream, irregularly concentrically purple-red lined towards base of tube with lines coalescing around corona but above reduced to blotches and spots, smooth and shiny towards base of tube, above densely papillate with slenderly conical or somewhat dorsiventrally compressed and obtuse to shortly apiculate papillae up to 1.0-1.2 mm long (max. length in mouth of tube); tube 6-11 mm diam., deeply cupular; lobes 5-7 mm long, 6-8 mm broad at base, erect to widely spreading, deltate, acute, sometimes with thickened erect papillate margin. Corona 4-5 mm tall, 4 mm broad, without basal stipe; outer lobes broadly triangular to bidentate, fused to base of tube in lower half, deep maroon; inner lobes 2.5 $\times$ 1.0 mm long, maroon streaked with pale yellow, below adpressed to backs of anthers, somewhat dorsiventrally flattened and broadened into transversely gibbous base, above $\pm$ terete, connivent, then (above middle) divergent and slightly tapering to obtuse or slightly clavate papillate-bristly apex.

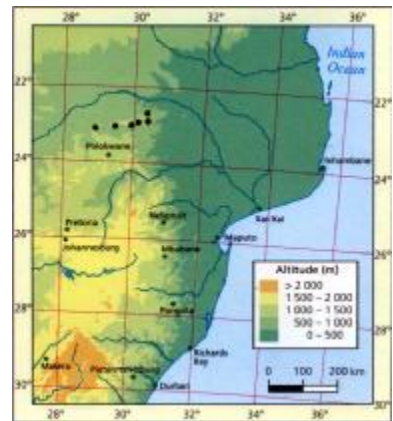


Fig. 5.208. Distribution of *Huernia whitesloaneana*.

HUERNIA WHITESLOANEANA

Distribution and habitat

Huernia whitesloaneana is endemic to the Blouberg and the Soutpansberg in the northernmost part of South Africa. In the Blouberg it is found at between 1 500 and 1 700 m on the plateau to the north of Buffelshoek. In the Soutpansberg it is widespread at about 1100-1 500 m and has been recorded from near Vivo in the west via the higher peaks just north of Louis Trichardt to some of the lower peaks north of Sibasa in the east.

Plants usually grow on much-weathered, more or less flat, sandstone outcrops on top of the mountains in very exposed spots. These are often inhabited by a wealth of other small succulents such as species of *Aloe*, *Crassula*, *Anacampseros*, *Euphorbia* and members of the Commelinaceae, but sometimes only by a small species of *Selaginella*. Specimens of *H. whitesloaneana* grow wedged tightly in narrow crevices in these rocks and manage to squeeze along them to form, in some cases, quite extensive plants with hundreds of minute stems, an example of which is shown in Dyer (1955).

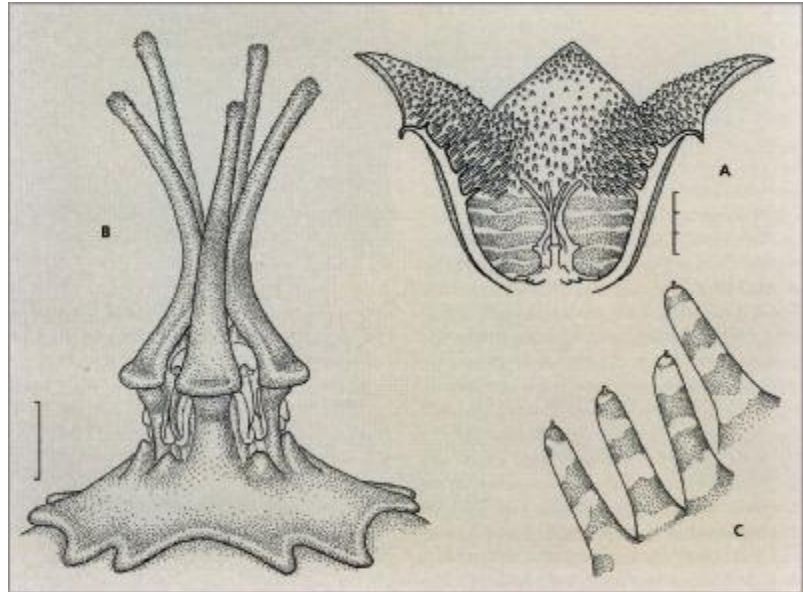


Fig. 5.209. *Huernia whitesloaneana*. A, side view of dissected flower. B, side view of gynostegium. C, papillae inside corolla in mouth of tube. Scale bars: A, 3 mm; B, 1 mm; C, 0.5 mm (at B). Drawn from A, PVB 6571, near Vivo, Soutpansberg; B, C, PVB 6997, Buffelshoek, Blouberg.



Fig. 5.210. *H. whitesloaneana*. PVB 6571, near Vivo, Soutpansberg.

Diagnostic features and relationships

Although their circumstances in habitat usually prevent them from forming substantial clumps, this happens readily to plants of this species in cultivation. *Huernia whitesloaneana* is one of the smallest-stemmed species in the genus and especially among the summer-rainfall species, which are generally robust in habit. The stems have a distinctive purplish green colour which they often retain in cultivation. This and their small size enables them to be distinguished quite easily from most other *Huernias* that occur in the area.

The flowers in *H. whitesloaneana* are small and may be only 10 mm long and 12 mm broad. They are quite variable in shape, from more or less cylindrical to quite widely gaping beyond the mouth of the tube, and this variation is present in most populations. They emit a slight, but sharp, bad odour. A distinctive feature of the flower is the manner in which the corolla lobes do not fold backwards much at their base, unlike in most other small-flowered species, and they continue the direction of the tube to their apices. The corolla is darkly spotted both inside and outside but these spots on the two surfaces are entirely independent of one another. On the inside the spots change to concentric lines in the lower half of the tube and coalesce into a dark patch around the corona. In many flowers this spotting is dense enough to make the whole inside appear dark but in some the spots are smaller and fewer and then the flower may be quite pale within. From about the middle of the tube to the tips of the lobes the inside of the corolla is covered with papillae. These have minute apical bristles, if any, and they decrease in length towards the tips of the lobes.



Fig. 5.212. *H. whitesloaneana*, PVB 6997, near Buffelskloof, Blouberg.



Fig. 5.211. *H. whitesloaneana*, PVB 6571, near Vivo, Soutpansberg, with darker flowers than usual.

The outer corona consists of very short, deep maroon lobes spreading on the base of the tube while the inner lobes are quite long and slender, tapering to obtuse, finely bristly tips. They are somewhat paler than the outer and are streaked with yellow.

History

Huernia whitesloaneana was discovered by G.C. Nel in June 1935 at the Entabeni Forest Station at an altitude of nearly 1 500 m in the Soutpansberg, somewhat east of Louis Trichardt. His collection flowered in March 1936 and he described it soon after, naming it in honour of Alain C. White and Boyd L. Sloane. It was first recorded on the neighbouring Blouberg by Dyer and Codd in January of 1955 (Dyer 1955).

33. *Huernia pillansii*

Huernia pillansii N.E.Br., Gard. Chron. Ser. 3, 35: 50 (1904).

Type: South Africa, Cape, 3 miles east of Matjiesfontein, N.S. Pillans 23 (BOL, holo.; GRA, K, iso.).

Small succulent forming dense to loose low clump up to 150 (-300) mm diam. Stems 15-60 (-180) mm long, 7-15 mm thick (excluding teeth), erect, $\pm$ cylindric or narrowly ovoid; tubercles 4-10 mm long, spreading, conical, arranged loosely in (9-) 10-16 (-24) vertical or sometimes spiralling rows, tapering into slender soft bristle 2-8 mm long. Inflorescence with 1-5 flowers developing in gradual succession on short peduncle; pedicel 2-8 mm long, 1 mm thick, ascending and holding flower facing upwards; sepals 8.5-12.5 mm long, narrowly ovate-attenuate. Corolla 30-50 mm diam.; outside yellowish to pinkish becoming cream towards base, smooth with 3 raised longitudinal veins on lobes and upper part of tube; inside densely papillate, cream to pale yellow densely and finely flecked with red or rarely uniformly red, covered except in lower half of tube with cylindric obtuse to slightly subclavate papillae to 1 mm long (longest at mouth of tube) sometimes tipped with minute bristle, papillae pale yellow banded and striped with red; tube 5-9 mm long, 6-8 mm broad at mouth, cupular to subcylindric; lobes 12-22 mm long, 6-8 mm broad at base, spreading to recurved, narrowly deltate, acuminate to attenuate. Corona $\pm$ 4 mm tall, 4 mm broad, dark maroon, without basal stipe; outer lobes fused to tube only at base, deltoid to broadly quadrate; inner lobes 1.8-2.5 mm long, erect, dorsiventrally much flattened, somewhat gibbous at widened base, tapering slightly to bristly clavate apex.

Distribution and habitat

Huernia pillansii is widely distributed in the southern parts of South Africa in the Little Karoo and on the south-western flank of the Great Karoo. It has been recorded from Montagu and near Touws River in the west to Camfers Poort in the east, which lies somewhat to the north-west of Steytlerville. It is probably most common around Matjiesfontein and between Ladismith and Oudtshoorn and is particularly plentiful around Calitzdorp.

Plants are always found in stony places under short bushes, sometimes on steep areas but usually on gentle slopes.



Fig. 5.213. *H. pillansii*, PVB 3719a, Bosluiskloof.

HUERNIA PILLANSII

Diagnostic features and relationships

With its rounded and hardly angled, almost 'furry' stems which are often densely packed into mats, *H. pillansii* is one of those stapeliads that is always immediately recognisable, whether flowers are present or not.

The stems are almost cylindrical and the tubercles are arranged very vaguely into anything between 10 and 16 rows, which often form spirals up the stem. As in several other species, the stems are extremely variable in length and relative thickness. They may be short (15-30 mm long) and nearly as thick as tall and then form dense, tightly packed mats, but they may also be quite long and slender and gathered into quite diffuse clumps. In *H. pillansii* (and *H. longii*) the number of angles rises rapidly on the primary stem from the initial number of four to the level typical of mature stems. Each tubercle is attenuated into a soft, bristle-like leaf-rudiment which tends to wear off with age.

In *H. pillansii* the flowers have long, narrowly deltate lobes which taper to a fine point and are usually at least three times as long as broad. There is a relatively short, cupular tube. The inner surface is cream, finely spotted with

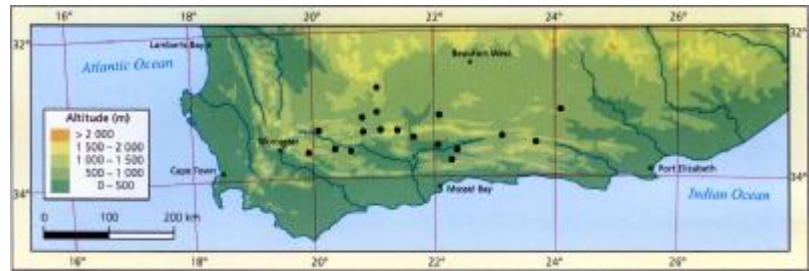


Fig. 5.214. Distribution of *Huernia pillansii*.

red (rarely uniformly red) and from a distance this has the appearance of being pale brown all over. It is covered with papillae which are of a similar size over the whole surface, though they decrease slightly in length towards the tips of the lobes. Inside the tube is a very darkly coloured gynostegium. This has relatively long outer lobes adpressed to the base of the tube and fairly long, erect inner lobes which end in a swollen and noticeably bristly apex.

Although the flowers of *H. pillansii* are unusual within the genus, they are similar to those of *H. longii*. These two species differ mainly in that *H. longii* has a distinctly rhizoma-

tous habit and, while the stems are also cylindrical, the tubercles are more clearly arranged into far fewer rows in *H. longii*. The slender bristles on the tubercles of *H. pillansii* are replaced in *H. longii* with a much shorter leaf-rudiment. Flowers of *H. longii* are similarly coloured but have distinctly shorter corolla lobes.

The stems of *H. pillansii* are also reminiscent of those of *Stapelianthus pilosus*. However, where *S. pilosus* is very unusual in this respect in *Stapelianthus*, in *Huernia* there is a graduation from 4-angled stems right through to the more or less cylindrical shape with large numbers of obscure angles that are found in *H. pillansii*.



Fig. 5.215. *H. pillansii*, PVB 1211, Calitzdorp Dam, in habitat, January 1985.

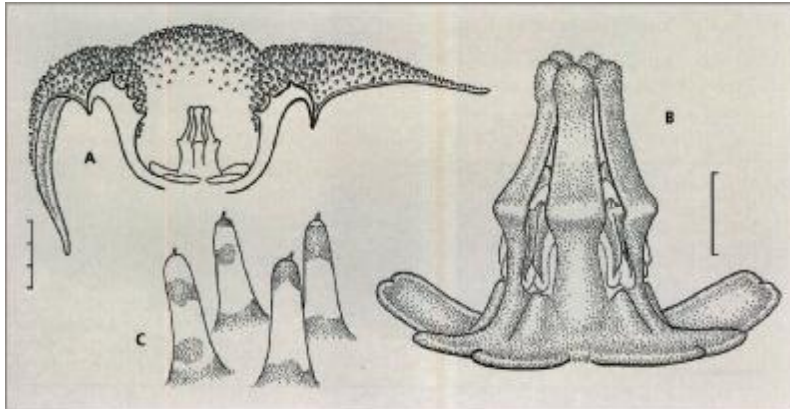


Fig. 5.216. *Huernia pillansii*. A, side view of dissected flower. B, side view of gynostegium. C, papillae inside corolla in mouth of tube. Scale bars: A, 3 mm; B, 1 mm; C, 0.5 mm (at B). Drawn from PVB 3719a, Bosluiskloof.

There is no similarity in the flowers, though, between *H. pillansii* and *S. pilosus* and the similarity of the stems appears to be purely coincidental.

History

Huernia pillansii was described from material collected by N.S. Pillans in stony places east of Matjiesfontein in 1902. He appears to have been the first to find it but it was then seen several times shortly after this, by Marloth in the same area in July 1903, by H. Bolus near Prince Albert in 1904, and by Eustace Pillans in 1906 at Oudtshoorn.



Fig. 5.217. *H. pillansii*, PVB 1211, Calitzdorp Dam.



Fig. 5.218. *H. pillansii*, Court, Matjiesfontein. Plant with short, stout stems (photo: G.D. Court).

34. *Huernia longii*

Huernia longii Pillans, J. S. African Bot. 5: 65 (1939).

Type: South Africa, Cape, Uitenhage District, Groendal, Long 1154 (BOL).

Small succulent usually consisting of clumps (up to 150 mm diam.) connected by underground rhizomes. Stems (above ground) 30-70 (-150) mm long, (3-) 5-15 mm thick, decumbent to erect above soil often from horizontal rhizomes 50-300 mm long, grey-green to reddish towards tips, ± terete, obtuse; tubercles 1.5-3.0 mm long, spreading, deltoid, ± conical and joined right near base into 6-9 often spiralling rows along stem, tapering abruptly towards middle into slender lanceolate tooth 1-2 mm long. Inflorescence of 1-5 flowers developing in gradual succession, arising near base of stem from small peduncle up to 7 mm long with slender acuminate bracts 2-3 mm long without lateral teeth; pedicel 2-8 mm long, 1.5 mm thick, spreading with upturned apex so that flower facing slightly upwards; sepals 4-7 mm long, ovate-acuminate. Corolla 20-30 (-35) mm diam., campanulate; outside smooth, pinkish to cream, with 3-5 longitudinal veins running down each lobe; inside cream densely spotted with red-brown becoming more finely spotted on whitish towards base of tube, covered on lobes and to halfway down tube with cylindrical ± obtuse papillae up to 1 mm long and usually horizontally banded with red-brown on cream, each with a small apical bristle; tube 8-9 mm long, 7-9 mm broad at mouth, cupular, cylindrical; lobes 5.5-10.5 mm long, 6-11 mm broad at base, spreading with apices recurved, deltate, acute. Corona 5.0-6.0 mm tall, 5.5-7.0 mm broad, without basal stipe; outer lobes 1.5-2.0 mm long, ± rectangular to deltoid and usually notched at apex, dark maroon; inner lobes 2.0-3.5 mm long, reddish becoming maroon towards apex, adpressed to backs of anthers near their base, dorsiventrally flattened below and somewhat dorsally swollen at base, above connivent then diverging above middle or remaining erect, becoming terete and tapering slightly to slightly swollen bristly-tuberculate apex.

Huernia longii is of restricted distribution in the southern parts of the Eastern Cape where it occurs in the Groot Winterhoek Mountains and in the south-eastern corner of the Baviaanskloof and Kouga Mountains.

Plants of *H. longii* grow on steep sandstone or conglomerate slopes with a host of other succulents (belonging to such genera as *Adromischus*, *Crassula*, *Euphorbia*, *Haworthia*



Fig. 5.219. *H. longii* subsp. *longii*, PVB 1824, Groendal, Uitenhage.

HUERNIA LONGII

and *Senecio*) in locally arid patches that are otherwise mainly surrounded by dry *fynbos*.

Huernia longii is unique in *Huernia* for the rhizomatous habit of the stems. These form groups from which the outer stems spread for up to 30 cm horizontally underground and then rise to the surface to form new clumps away from the parent plant. Along the stems the tubercles are arranged into 6-9 clear rows which are often slightly spiraled. Each tubercle is tipped by a small tooth which gradually wears off with age. The stems bear a remarkable resemblance to those of, say *Echidnopsis montana* and share with this species also the rhizomatous habit. Florally, *E. montana* is, of course, very different.

Florally *H. longii* and *H. pillansii* are very similar. In *H. longii* the corolla lobes vary from a little longer than broad to twice as long as broad but do not taper into slender tips. The shape of the tube and the spotting of red-brown on cream inside the flower are also very similar to those of *H. pillansii*. As in that species, there are papillae all over the corolla to about halfway down the tube where they abruptly end and they are banded with red-brown on cream. The outer corona is indistinguishable from that in *H. pillansii* and is also dark maroon, while in the inner corona there is some variation, on the basis of which two subspecies are recognised: in both it has a swollen, bristly apex. In *H. longii* the flowers emit a faint excrement-like odour.

Leach (1988) did not really address the problems that I had raised (Bruyns 1984) with his placing of *H. echidnopsioides* as a subspe-

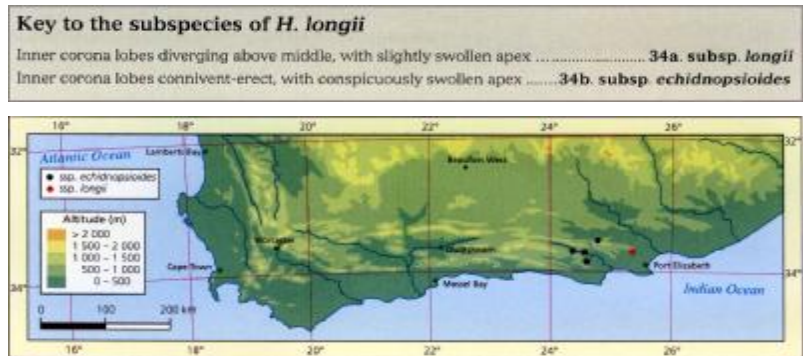


Fig. 5.220. Distribution of *Huernia longii*.

cies of *H. pillansii* and, in his revision of *Huernia*, he opted for the other possibility suggested in that paper, which was to raise all three taxa to specific level. He informed me once as well that he had not been aware of *H. longii* when he described *H. pillansii* subsp. *echidnopsioides*. However, the differences between '*echidnopsioides*' and '*longii*' lie only in the different orientation of the upper parts of the inner corona lobes and this is not consistent with his treatment of *H. hystrix* and its var. *parvula* (where the differences in the coronas are more considerable and they are also accompanied by differences in the stems). I have therefore reverted to my arrangement of two subspecies of *H. longii*.

34a. *Huernia longii* subsp. *longii*

Inner corona lobes connivent then diverging above middle, with slightly swollen apex.

Distribution and habitat

Huernia longii subsp. *longii* is only known to occur in the semi-arid lower reaches of the Kwa-Zungu River valley to the north of Uitenhage. Here it occurs on steep, crumbly conglomerate slopes between the higher sandstone mountains.

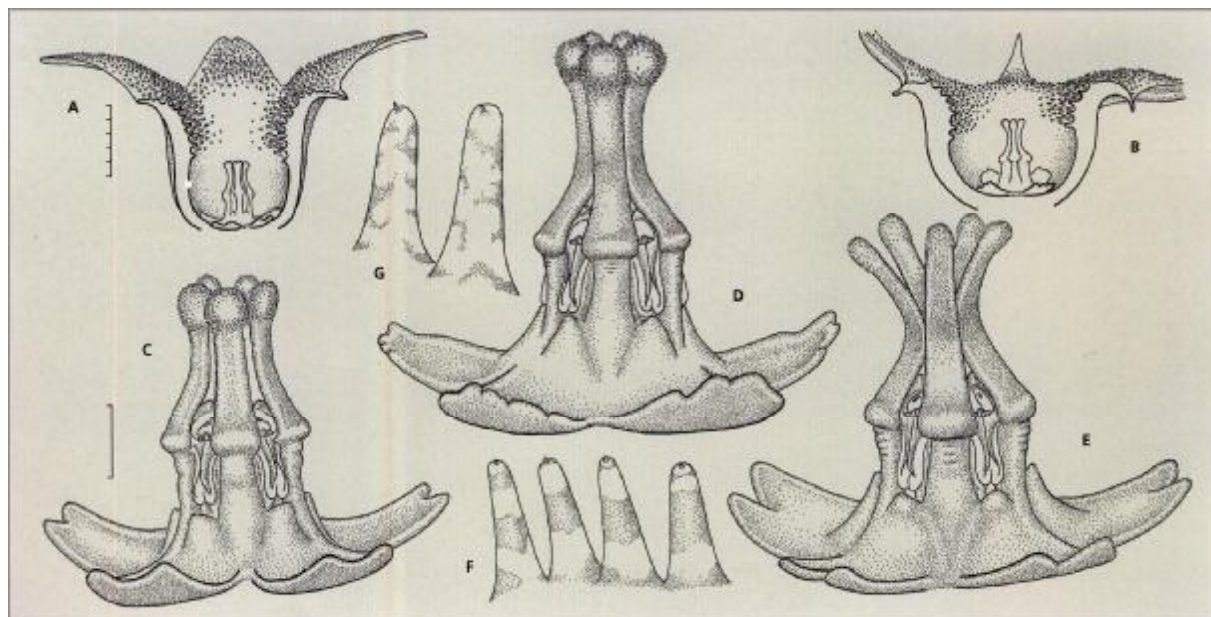


Fig. 5.221. *Huernia longii* (E, subsp. *longii*; rest subsp. *echidnopsioides*). A, B, side view of dissected flower. C-E, side view of gynostegium. F, G, papillae inside corolla in mouth of tube. Scale bars: A, B, 5 mm (at A); C-E, 1 mm (at C); F, G, 0.5 mm (at C). Drawn from A, C, F, PVB 1838, west of Patensie; B, D, G, PVB 7042, near Cockscomb Peak, south of Steytleville; E, PVB 1824, Groendal, Uitenhage.



Fig. 5.222. *H. longii* subsp. *longii*, PVB 1824, Groendal, Uitenhage, growing among pebbles on steep, conglomerate slopes, December 1978.

Diagnostic features and relationships

The inner corona lobes provide the only reliable means of distinguishing the two subspecies of *H. longii*. Leach (1976a) gave a series of differences between these two taxa but these were shown in Bruyns (1984) to be of no help in separating them. In subsp. *longii* the inner corona lobes diverge above the middle and have only a slightly swollen apex. In subsp. *echidnopsioides* they remain connivent above the middle and usually have a slightly more swollen apex.

History

Subsp. *longii* was first discovered in 1939 by Frank R. Long, the director of parks in Port Elizabeth between 1929 and 1940 who collected several interesting succulents in that area, many for the first time. His collection was from the steep sides of the valley leading up to the Groendal Dam (Long 1948), which lies in the mountains to the north of Uitenhage, and this is where all subsequent collections have been made of this taxon.

34b. *Huernia longii* subsp. *echidnopsioides*

Huernia longii subsp. *echidnopsioides* (L.C. Leach) Bruyns, *Bradleya* 2:18 (1984).
Huernia pillansii subsp. *echidnopsioides* L.C. Leach, *J. S. African Bot.* 34:140 (1968).
Huernia echidnopsioides (L.C. Leach) L.C. Leach, *Excelsa Taxon. Ser.* 4: 51 (1988).

Type: South Africa, Cape, Baviaans Kloof, Leach & Bayliss 13612 (PRE, holo.; K, SRGH, iso.).

Inner corona lobes usually connivent-erect, with conspicuously swollen apex.

Distribution and habitat

Subsp. *echidnopsioides* is found at the south-eastern end of the Baviaanskloof and Kouga Mountains, where it grows in the hills to the west and south-west of the small town of Patensie. It has also been collected on the northern slopes of the Groot Winterhoek range near Cockscomb Peak, to the south of Steyterville.

History

Subsp. *echidnopsioides* appears to have been recorded for the first time by Frank J. Stayner in 1962. Although thought to occur only along the road that runs into the Baviaanskloof west of Patensie, it is in fact plentiful on many of the higher areas to the south of this towards the Long Kloof and it also occurs as far west as the Paul Sauer Dam on the Kouga River. In 1997 was it collected for the first time south of Steyterville in the Groot Winterhoek Mountains, well outside the area from which it was traditionally known.

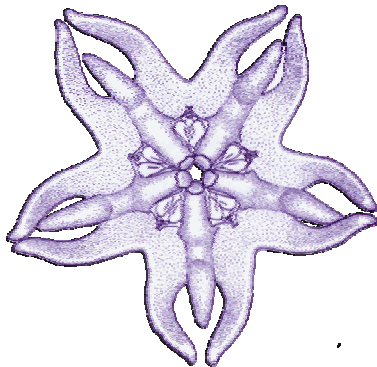


Fig. 5.223. *H. longii* subsp. *echidnopsioides*, PVB 7124, near Kareedouw.



Fig. 5.224. *H. longii* subsp. *echidnopsioides*, PVB 7042, near Cockscomb Peak, south of Steyterville.

6. *Larryleachia*



The first species of *Larryleachia* to become known was described as *Stapelia clavata* and was discovered by William Paterson, probably at Geselskapbank in western Bushmanland in September 1778 (Brown 1907-09). This peculiar plant was described without flowers, so it is impossible to match it with certainty to any

of the species known today. However, it is possible that it is the same as *L. cactiformis*, which occurs today at Geselskapbank and seems to be the only species there. Carl Zeyher collected a similar plant between 1829 and 1831, probably in the Kamiesberg or west of the escarpment in the coastal hills of Namaqualand. This flowered at Kew and was described by W.J. Hooker as *Stapelia cactiformis*.

N.E. Brown placed this species under *Trichocaulon* since he could find no structural difference in the flowers between it and others with spiny stems (*T. flavum*, *T. piliferum*) on which he had founded *Trichocaulon* (Brown 1890, t. 1905). White & Sloane (1937) listed 13 'species' of 'smooth-stemmed' *Trichocaulon*. Plowes (1978a) made some vague suggestions for reducing the number of names in this group and this problem was addressed very much more seriously and carefully by D.T. Cole in an essay on the subject (Cole 1979) which was reprinted later with slight changes (Cole 1984). Cole (1979) concluded that, apart from the poorly known *T. sociarum*, there were four

species: *T. cactiforme*, *T. marlothii*, *T. perlatum* and *T. simile*. He noted the existence of what was possibly a new species but, at that stage, needed to 'collect more material and to carry out a good deal of further study' to make sure. This new species was later described as *Trichocaulon felinum* (Cole 1985). He also pointed out for the first time that many of the illustrations in White & Sloane (1937) and Lückhoff (1952) were incorrectly identified. Cole's suggestions have to a very large extent been confirmed by more recent studies in the group (Bruyns 1993). It is most unfortunate, however, that of the apparently large amount of material that he examined, apart from the type of *T. felinum*, no herbarium specimens seem to have been prepared from the plants and consequently none of his statements are verifiable.

The genus *Trichocaulon* consisted of some spiny species and the 'smooth-stemmed' species, which are vegetatively of quite different appearance. With the increasing use of vegetative characters in the classification of the stapeliads, *Trichocaulon* was split up and

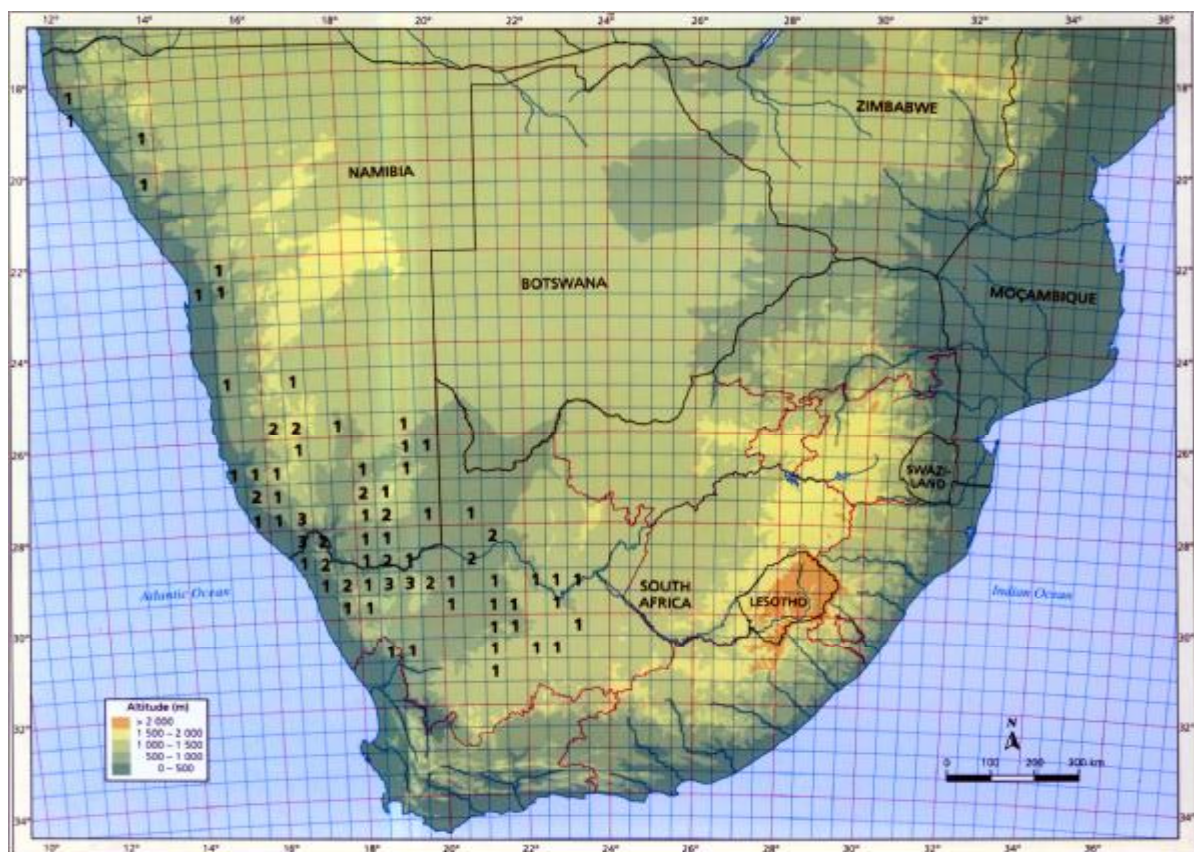


Fig. 6.1. Patterns of diversity in *Larryleachia*, showing the number of species recorded to date in each half-degree square.

the spineless species were accommodated in *Lavrania* (Bruyns 1993).

Plowes has made three attempts to solve the problem posed by the generic placing of the so-called 'smooth-stemmed' species of *Trichocaulon* by describing the new genera *Leachia*, *Leachiella* and *Larryleachia* to accommodate them. The first two of these names have both turned out to be illegitimate: the first is a later homonym of *Leachia* (Asteraceae) and the second of *Leachiella* (Rhodophyceae). His latest article (Plowes 1996), in addition to describing yet another genus, *Larryleachia*, makes several changes but without any scientific argument or evidence put forward to support them. This genus is accepted here but not for the reasons given by Plowes (Bruyns 1999c). These reasons are discussed further under *Lavrania*. Our molecular investigations have shown that *L. tirasmontana* is not closely related to *L. picta* and so it is treated as a separate species here, rather than as a subspecies of *L. picta*. They also indicate that the two winter-rainfall species *L. cactiformis* and *L. perlata* are sisters but the relationships among the others are unresolved.

Larryleachia Plowes, *Excelsa* 17: 5 (1996). Type: *Larryleachia cactiformis* (Hook.) Plowes.

Lavrania sect. *Cactoidea* Bruyns, *S. African J. Bot.* 65:305 (1999).

Type: *Lavrania cactiformis* (Hook.) Bruyns.

Leachia Plowes, *Asklepios* 56:11 (1992), nom. illegit., non Cassini (1822).

Type: *Leachia cactiformis* (Hook.) Plowes.

Leachiella Plowes, *Asklepios* 57:15 (1992), nom. illegit., non Kugrens (1892).

Type: *Leachiella cactiformis* (Hook.) Plowes.

Hoodia sect. *Cactoidea* Halda, *Acta Mus. Richnov. Sect. Natur.* 5: 31 (1998).

Type: *Hoodia cactiformis* (Hook.) Halda.

Spineless non-rhizomatous succulent consisting of 1 to many stems forming small shrub up to 300 mm tall. Stems 20-65 mm thick, erect to rarely spreading, cylindrical clavate to nearly spherical, fleshy and firm, glabrous, grey-green; tubercles mostly < 3 mm long, flattened rounded polygonal, covering stem and arranged roughly into 12-19 rows along stem, each tipped with small dorsiventrally flattened persistent leaf-rudiment < 1 mm long usually sunken into depression near apex, without stipular denticles. Inflorescences glabrous, up to 30 or more per stem, arising mainly towards apex, bearing 1-6 (-12) flowers opening in succession (rarely simultaneously), forming peduncular patches with many narrowly deltoid bracts (often with lateral teeth near base) and basal bract seated on tubercle like those on stem; pedicel 0.5-2.0 mm long, $\pm$ 1 mm thick, generally spreading and holding flower facing out from stem; sepals 1.5-2.0 mm long, 0.5-1 mm broad at base, overlapping slightly at bases, occasionally with ciliate margins, deltate, acute. Corolla (5-) 6-16 mm diam., shallowly campanulate, rotate or

with strongly reflexed lobes, deeply lobed; outside glabrous and smooth; inside glabrous, smooth to papillate, papillae dome-like to obtusely conical and usually tipped with a short apical bristle; tube up to 3 mm deep, mostly shallow; lobes 2-6 mm long, 2-5.5 mm broad at base, spreading, ovate-deltate to lanceolate, convex above from reflexed margins, margins eciliate. Corona 1.5-3.0 mm tall, 2.0-6.0 mm broad, consisting of 2 series arising on staminal tube, glabrous, $\pm$ sessile at base of corolla tube; outer lobes erect, emarginate to deeply bifid into usually ascending lobules, laterally fused with bases of inner lobes and forming small pouch, dorsiventrally flattened and often channelled down inner surface; inner lobes adpressed to backs of anthers for most of anthers' length, sometimes exceeding them and rising in centre in small column, dorsiventrally flattened, with dorsal process fused into cup with outer lobes or forming discrete spreading obtuse lobule in series with outer lobules. Anthers horizontal on top of style-head, margins shrinking back to expose pollinia, rectangular. Pollinium D-shaped, longer than broad, insertion-crest twisting from outer edge onto dorsal surface, caudicle attached with $\pm$ broad cupular pad to base. Follicles erect to spreading against stems, teretefusiform, obclavate, slender to stout, consisting of 2 horns diverging at 30-180°, longitudinally flecked with purplish on paler background, glabrous, smooth.

In *L. marlothii* the plant always consists of three stems at least and may have up to 30; in *L. perlata* it may form a shrublet with up to eight stems but may remain single-stemmed; and in the remaining three species, *L. cactiformis*, *L. picta* and *L. tirasmontana*, it usually consists of a single, erect stem only. The stems themselves are usually 150 mm or less in height and only occasionally reach 300 mm in *L. perlata*. There is therefore a clear trend in the genus towards a dwarf, caetoid growth form. This entails reduction in the number of stems, reduction in their length and also an increase in their thickness.

The stems in *Larryleachia* are covered with tubercles which are round, usually broader than tall and often somewhat polygonal in outline. They are only slightly joined together into longitudinal rows. Even in young stems that have not borne flowers, the number of these rows is often hard to count. Up to 19 rows may occur but 12-16 is the more usual range. Each tubercle has a rounded-truncate summit, usually with a depression a little above the centre in which the leaf-rudiment is situated. These minute rudimentary leaflets are persistent and permanently soft. They are almost conical to obviously dorsiventrally flattened, slightly to markedly sunken into a pit, and a slight midrib may be visible dorsally on them.

The surface of the stem is papillate and many of the epidermal cells have their outer walls raised into a rounded papilla. Groups of these cells may be raised into 'hills' with the stomata sometimes deeply sunken between them.

Flowers are mainly produced towards the

apex of the stem and usually appear on the primary stem after two or three years or more. Large numbers of inflorescences arise. Older inflorescences from previous seasons (now lower down on the stem) quite often continue to bear, so flowers are found over most of the surface of the stem, though they are mainly concentrated towards the apex. Most of the inflorescences are small and bear only a few flowers, which develop successively except in *L. perlata* where several may open simultaneously on one inflorescence. With repeated use over several seasons, an inflorescence may develop into a large 'peduncular patch'.

The corolla is small, slightly campanulate with relatively deeply divided lobes, and it is held close to the stem on a very short pedicel. The corolla is slightly thickened around the mouth of the small tube in *L. cactiformis*, *L. picta* and *L. tirasmontana*, but not in *L. marlothii* or *L. perlata*. In *L. perlata* there appears to be an annulus but dissection shows that this is caused by folding in the corolla at the base of the lobes, similar to that seen in several species of *Huerfania*. The inside of the corolla is smooth in *L. marlothii* but densely papillate in all the others. These papillae are very low and rounded in *L. picta* and *L. tirasmontana*, but become conical and tipped with a conspicuous apical bristle in *L. cactiformis* and *L. perlata*. In *L. perlata* the apical bristle is unusual in that it is horizontal, thick and cylindrical with rounded ends.

In *Larryleachia* there is more or less no stipe beneath the gynostegium, so it flows into the base of the corolla tube. There are, as usual, two series of corona lobes. The outer series of lobules join up around the gynostegium to form a cupular structure with five deep bays beneath the guide-rails, which sometimes reach nearly to the base of the gynostegium. The inner lobes are mostly just flat on the anthers but rise in the centre in a column in *L. marlothii*, *L. picta* and *L. tirasmontana*. In some cases (*L. cactiformis*, *L. picta* and *L. tirasmontana*) there is a dorsal horn behind each inner lobe. The fact that it is often slightly laterally flattened suggests that this dorsal horn is derived from the inner lobes.

In *L. marlothii* the follicles are slender (3-6 mm thick) and diverge from each other at 30-60°. The seeds are relatively few, greyish, comparatively large ($\pm$ 6 mm long) and flat. They exhibit the unique phenomenon (in the stapeliads) of a narrow band of hairs, slightly shorter than the hairs of the coma, extending from the micropyle to halfway around each side along the base of the raised margin. In this species also the coma detaches from the seed somewhat reluctantly. In the others the follicles are much stouter (up to 10 mm thick) and the seeds are darker brown to almost black. In *L. picta* and *L. tirasmontana* the horns diverge at 30-60° but in *L. perlata* (fig. 36 C) and *L. cactiformis* they frequently diverge at over 180° and are parallel to or adpressed to the

LARRYLEACHIA MARLOTHII

surface of the stem (often curving up towards the apex of the plant while remaining parallel to its surface). In *L. cactiformis* the horns are often only 20-30 mm long but still bear a remarkable number of the small seeds, which are about 3 mm long. In *L. picta*, *L. perlata* and *L. tirasmontana*, the seed is also flat but in *L. cactiformis* the tiny, pear-shaped seed is folded tightly lengthways so that the cream border is mostly folded out of sight.

In *L. marlothii*, *L. picta*, *L. perlata* and *L. tirasmontana*, the seedling has a relatively broad, flat, more or less parallel-sided hypocotyl. In *L. marlothii* the cotyledons are broad, semicircular and flat, while they are more succulent and more broadly attached to the hypocotyl in *L. perlata*, *L. picta* and *L. tirasmontana*. In *L. cactiformis* the plantlet is stout and fat, sometimes almost spherical, and the cotyledons are tiny, very succulent, scarcely separated from the apex of the hypocotyl and very close together on its apex.

The various species of this genus may be quite difficult to distinguish and one may be excused sometimes for wondering whether this is not perhaps a single, variable taxon, as Huber (1967) considered them all to be. However, although the characters of the flowers can occasionally be misleading (especially between *L. cactiformis*, *L. picta* and *L. tirasmontana*), this is one case among the stapeliads where characteristics of the seed and seedlings are useful if they can be observed. These and the features of the distribution (where certain taxa are sympatric and retain their distinctness) show that one is dealing here with five distinct species, as mooted in part by Cole (1979).

Like *Hoodia*, *Larryleachia* is found only in arid to very arid situations and is particularly associated with the Namib Desert (though the records are very scanty north of Lüderitz) and with the lower valley of the Orange River, along which it also advances furthest to the east.

Larryleachia marlothii covers nearly the whole distribution area, with the papillate-flowered taxa occurring more or less sympatrically with it: *L. cactiformis* and *L. perlata*

in the winter-rainfall zone, and *L. picta* and *L. tirasmontana* in the summer-rainfall parts. The distribution is relatively concentrated and, despite there being only five species, up to three are found growing near one another. This occurs among the quartz hills in the vicinity of Pofadder (*L. cactiformis*, *L. marlothii*, *L. picta*) in the Northern Cape and around Rosh Pinah in south-western Namibia (*L. marlothii*, *L. perlata*, *L. picta*).



Fig. 6.2. *L. marlothii*, PVB 1319, east of Alexander Bay, Richtersveld.

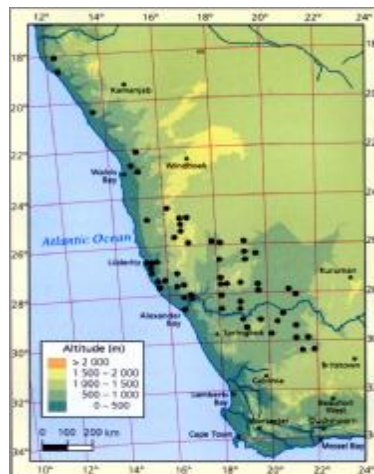


Fig. 6.3. Distribution of *Larryleachia marlothii*.

1. *Larryleachia marlothii*

Larryleachia marlothii (N.E.Br.) Plowes, *Excelsa* 17: 7 (1996).

Trichocaulon marlothii N.E.Br., *Fl. Cap.* 4 (1): 894 (1909).

Leachia marlothii (N.E.Br.) Plowes, *Asklepios* 56:12 (1992).

Leachiella marlothii (N.E.Br.) Plowes, *Asklepios* 57:16 (1992).

Lawrania marlothii (N.E.Br.) Bruyns, *S. African J. Bot.* 59: 342 (1993).

Hoodia marlothii (N.E.Br.) Halda, *Acta Mus. Richnov. Sect. Natur.* 5: 31 (1998).

Type: South Africa, near Kenhardt, *Marloth* 3763 (missing).

Neotype: *Fl. Pl. South Africa* 18: t. 681 (1938).

Trichocaulon dinteri A.Berger, *Stap. u. Klein.* 30 (1910).

Leachia dinteri (A.Berger) Plowes, *Asklepios* 56:12 (1992).

Leachiella dinteri (A.Berger) Plowes, *Asklepios* 57:16 (1992).

Larryleachia dinteri (A.Berger) Plowes, *Excelsa* 17: 5 (1996).

Hoodia dinteri (A.Berger) Halda, *Acta Mus. Richnov. Sect. Natur.* 5: 31 (1998).

Type: Namibia, Kalkhügel in der Namib 82 km östlich Swakopmund, *Dinter* 3136a (SAM).

Trichocaulon keetmanshoopense Dinter, *Neue Pflanzen Deutsch-SWA's* 57 (1914).

Type: Namibia, zwischen Keetmanshoop und Aroab auf Karooschiefer in der Rhigozum-Steppe, Jan. 1910, *Dinter* 3258 (missing).

Trichocaulon sinus-lüderitzii Dinter, *Neue Pflanzen Deutsch-SWA's* 59 (1914).

Type: Namibia, auf Strandfelsen, nördlich von Lüderitzbucht, zuerst 1897 wieder Jan. 1910 gesammelt, *Dinter* 3163 (missing).

Included in the present concept of *L. marlothii* are Figs. 1101, 1107, 1109, 1111, 1112 (left only) of White & Sloane (1937) and Plate XXXII d of Albers & Meve (2002).

Key to the species

1. Corolla lobes strongly reflexed and pressed against stem, margins folded back, papillae on inner surface each tipped with horizontally spreading cylindrical obtuse bristle 2. *L. perlata*
1. Corolla not as above, papillae if present without apical bristle or apical bristle erect and very minute 2.
2. Flowers entirely without papillae inside, inner corona mostly lacking dorsal projection 1. *L. marlothii*
2. Flowers papillate inside, at least in mouth of corolla tube, inner corona with conspicuous dorsal projection confluent with horns of outer lobes 3.
3. Inner corona lobes either horizontally adpressed to anthers and scarcely exceeding them or just meeting in centre but not rising in column in centre 4.
4. Corolla inside with purple to red spots on pale background and dark patch on apex of lobes, horns of outer lobes strongly diverging, plants from Namibia north of Aus 5. *L. tirasmontana*
4. Corolla inside with purple-red bars on pale background to ± uniformly purple-red or maroon (without dark apical patch), horns of outer corona lobes nearly straight, plants from south of Orange River 3. *L. cactiformis*
3. Inner corona lobes usually meeting in centre and there rising into column taller than height of outer corona lobes 4. *L. picta*

Dwarf shrub with 3-30 stems, branching from base. Stems 30-150 mm long, 20-55 (-65) mm thick, erect to spreading, cylindrical clavate or ovoid; *tubercles* flattened rounded polygonal, crowded but arranged into $\pm$ 12-19 rows along stem, each tipped with small conical to flattened leaf-rudiment < 1 mm long seated in a small depression. *Inflorescences* mainly in upper parts of stem but sometimes evenly spread over plant, with flowers in groups of 1-5, developing successively; *pedicel* $\pm$ 1 mm long, 1 mm thick; *sepals* 1.5-2.0 mm long, 1 mm broad at base, ovate, acute. *Corolla* 8-16 mm diam., campanulate to $\pm$ rotate; outside green spotted with reddish; inside variously mottled with red to dark red-brown on cream background, sometimes nearly uniformly dark purple-brown (in north), smooth; *tube* 0.5-3.0 mm deep, very shallowly saucerlike to cupular, with corolla scarcely to not at all thickened

at mouth; *lobes* 2-5 mm long, 3-5 mm broad at base, spreading, often with recurved tips, broadly ovate-deltate, acute, margins slightly to not at all recurved. *Corona* 2-3 mm tall, 3.5-1.5 mm broad, irregularly spotted and lined with pink to maroon on cream background, often with droplets of nectar accumulating on upper surfaces, sessile; *outer lobes* 1.5-2.0 mm long, ascending, bifid to well below middle into slender sometimes nearly terete widely divergent spreading to ascending obtuse lobules, laterally fused towards base with bases of inner lobes to form pouch; *inner lobes* 1.5-2.0 mm long, adpressed to backs of anthers and exceeding them then connivent-erect and rising into column in centre sometimes diverging at tips, linear, obtuse, occasionally with small obtuse dorsal projection near base and in series with outer lobes.

Distribution and habitat

Larryleachia marlothii is the most widely distributed species in the genus. It occurs along practically the whole length of Namibia from near the mouth of the Kunene River to the Orange River (it may well exist in Angola too), in and on the fringes of the Namib Desert. It is found more or less throughout the dry southern part of Namibia and extends eastwards as far as Upington and Vanwyksvlei in South Africa. Plants are quite common and characteristic in some of the coastal regions of the southern Namib, especially along the Orange River from the Lorelei (Kahanstal) to Alexander Bay and northwards to Lüderitz.

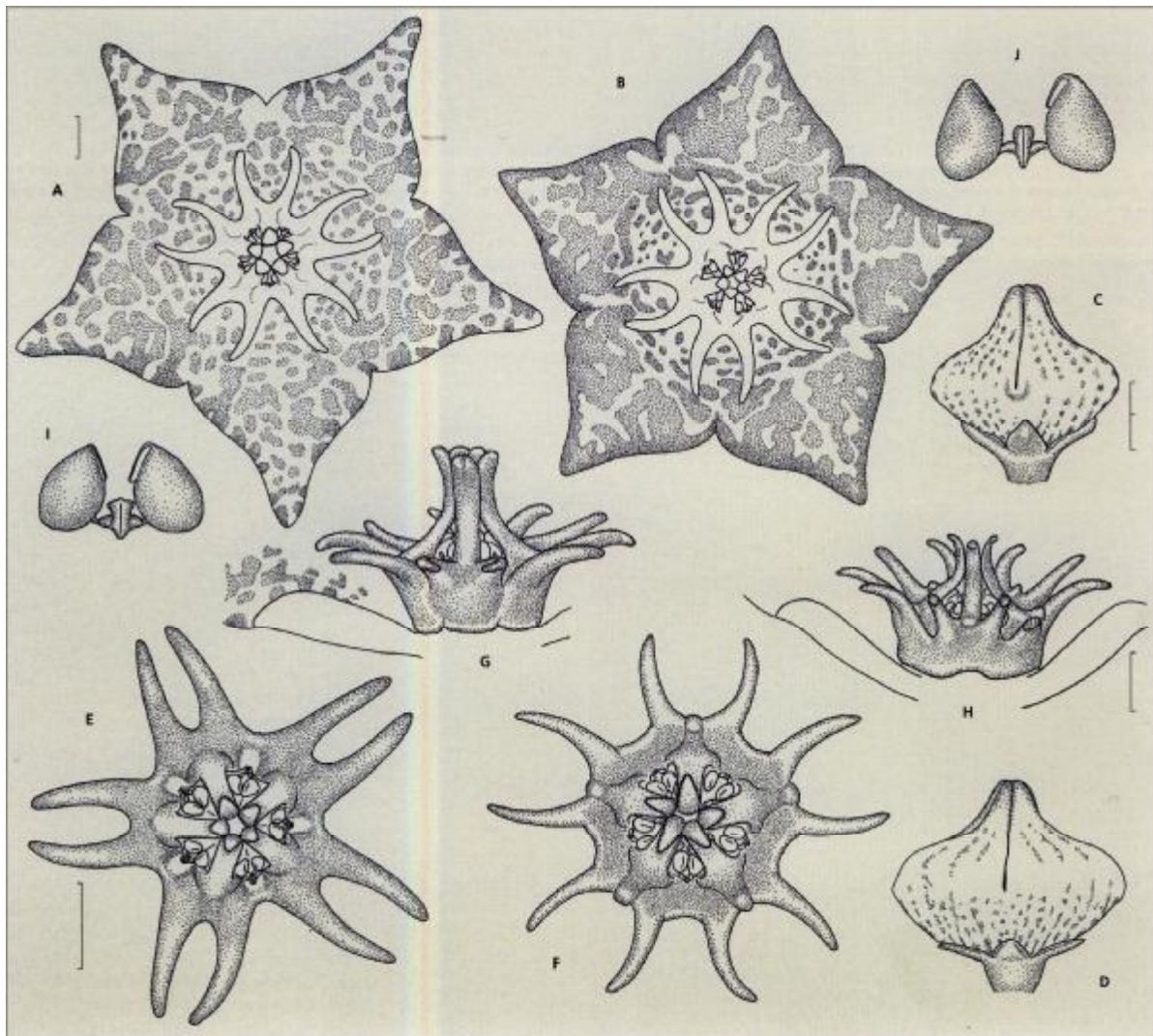


Fig. 6.4. *Larryleachia marlothii*. A, B, face view of flower. C, D, bud. E, F, face view of gynostegium. G, H, side view of gynostegium. I, J, pollinarium. Scale bars: A, B, 1 mm (at A); C, D, 2 mm (at C); E, F, 1 mm (at E); G, H, 1 mm (at H); I, J, 0.25 mm (at C). Drawn from: A, G, PVB 3478, north of Upington; B, PVB 3571, Springboktrek Suid, near Koës, Namibia; C, PVB 3569, near Koës, Namibia; D, Pretorius, Eendorn, Namibia; E, I, Heunis & Bruyns 28, near Aurus Mountains, Namibia; F, H, J, Kratz, south-east of Aus, Namibia.

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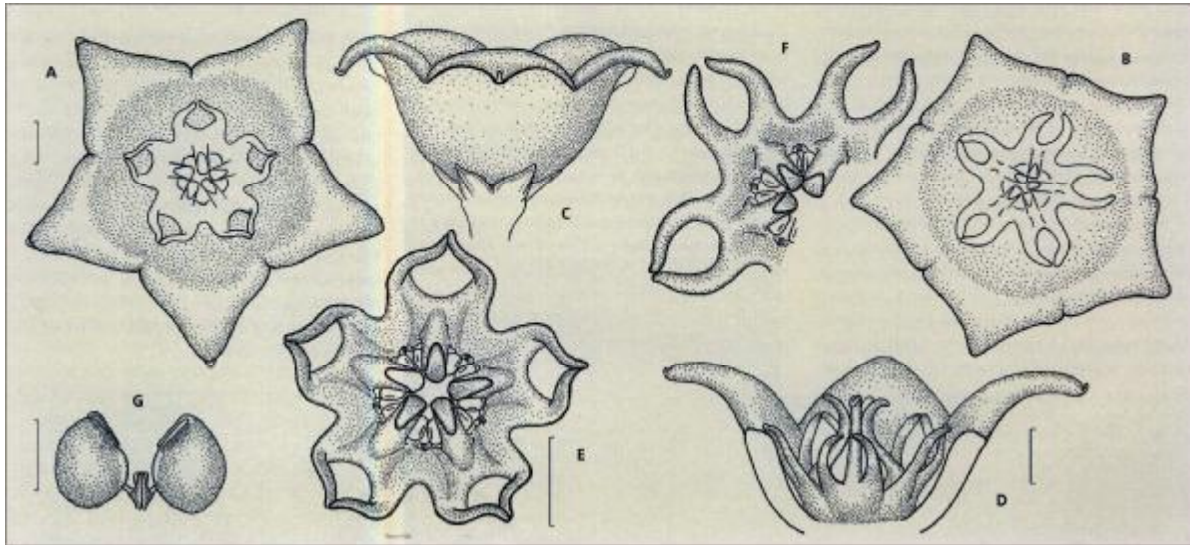


Fig. 6.5. *Larryleachia marlothii*. Material from north of Swakopmund formerly known as *Trichocaulon dinteri*. **A, B**, face view of flower. **C**, side view of flower. **D**, side view of dissected flower. **E, F**, face view of gynostegium. **G**, pollinarium. Scale bars: A-C, 1 mm (at A); D, 1 mm; E, F, 1 mm (at E); G, 0.25 mm. Drawn from: A, D, E, G, *Russel* 39, east of Torra Bay, Namibia; B, C, F, *Van Rensburg*, near Brandberg West, Namibia.



Fig. 6.6. *L. marlothii*, PVB 4172, south-west of Maltahöhe, Namibia.

In such places the plants mostly grow in the shelter of small stones in flat, windswept places with sand often filling many of the spaces between the stones and sometimes even partially covering the plants. Further east they occur under *Rhigozum trichotomum* bushes in flat gravelly or sandy areas. Around Pofadder the species has been seen a few times growing close to plants of *L. picta* and *L. cactiformis*: nevertheless they appear to be edaphically quite discrete, with *L. marlothii* on the sandier areas and the others on hard ground among quartz pebbles.



Fig. 6.7. *L. marlothii*, PVB 7902, a medium-sized specimen near the Klinghardt Mountains in the Namib Desert, south of Lüderitz, Namibia, July 1999.

Diagnostic features and relationships

Larryleachia marlothii is quite variable over this vast distribution. In the eastern part of its range the plants are usually more slender with a dark grey colour and deep grooves between the tubercles. They usually have at least three stems and may have up to 30 in some instances, then forming quite a robust clump, though the stems are mostly short and rarely exceed 100 mm long. The corolla lobes are relatively long and narrow (with a broad base) and the whole corolla has a characteristic reddish patterning on a cream background which varies only slightly in intensity. In the southern, winter-rainfall part of the Namib plants are mostly not more than 60 mm tall, with three to five stems, though even here occasionally they may have up to 20 stems, as was observed by Cole (1979). The harshness of the conditions here is indicated by the manner in which the stems are usually at least partially covered with a pale grey, corky layer caused by blasting by wind-borne sand. They are also thicker and the tubercles are much flatter, with hardly any grooves between them.

In the southern coastal Namib, from Lorelei towards Alexander Bay and northwards to Lüderitz, considerable variation is found in the colour patterns on the corolla. The corolla is also very variable in shape in this area, from nearly flat to quite obviously campanulate.

In the northern part of the range, from Swakopmund northwards, the corolla is more often campanulate. It is also smaller, with shorter, more deltate lobes and is frequently



Fig. 6.8. *L. marlothii*, PVB 3478, north of Upington.



Fig. 6.9. *L. marlothii*, Russel 39, east of Torra Bay, Namibia.



Fig. 6.10. *L. marlothii*, Van Rensburg, near Brandberg West, Namibia.

more darkly coloured, in some cases even a nearly uniform purple-black. However, even among these plants there is considerable variability and more or less flat flowers with red on cream may be encountered.

From the other species *L. marlothii* may often be distinguished by its more slender, dark grey stems with deep grooves around the tubercles which give the strong impression of an irregular arrangement of maize kernels 'on the cob'. However, this distinctiveness breaks down as one moves out of the *Rhigozum-Steppe* westwards into the Namib. *Larryleachia marlothii* is distinguished from all others in the genus by the fact that the corolla is entirely free of papillae and by the nearly total lack of any dorsal projection on the inner corona lobes,

though a minute, round one may occasionally be present. The striking distinctiveness of the seed, in which hairs arise along the margin for some distance away from the coma at the micropylar end, is unique among the stapeliads.

History

Larryleachia marlothii was first collected by M. Kurt Dinter near Lüderitz in 1897. These plants were given the name *Trichocaulon sinus-lüderitzii* but they were described later than *T. marlothii*, which came from near Kenhardt. Further names were given to a plant from east of Swakopmund (*T. dinteri*) and another one from Keetmanshoop (*T. keetmanshoopense*). It

was mooted by Plowes (1978a) and suggested more definitely by Cole (1979) that all of these were representatives of a single variable species. Cole (1979) also made the interesting observation that, in different seasons, plants could produce flowers of different sizes and that flowers even varied from flat to campanulate on a single plant. Since these are exactly the differences which could be used to separate '*marlothii*', the inland form and '*dinteri*', the form from the coastal Namib, all the evidence seems to suggest that Cole was correct and that one cannot distinguish further taxa within this species on the basis of the size of the flower and the shape of the corolla.



Fig. 6.11. *L. marlothii*, PVB 8060, south-west of Orupembe, Skeleton Coast, Namibia.

LARRYLEACHIA PERLATA

2. *Larryleachia perlata*

Larryleachia perlata (Dinter) Plowes, *Excelsa* 17: 9 (1996).

Trichocaulon perlatum Dinter, *Feddes Repert. Spec. Nov. Regni Veg.* 19:155 (1923).

Leachia perlata (Dinter) Plowes, *Asklepios* 56:14 (1992).

Leachiella perlata (Dinter) Plowes, *Asklepios* 57:16 (1992).

Lavrania perlata (Dinter) Bruyns, *S. African J. Bot.* 59: 342 (1993).

Hoodia perlata (Dinter) Halda, *Acta Mus. Richnov. Sect. Natur.* 5: 32 (1998).

Type: Namibia, Klinghardt mountains, at various places, fl. Sept. 1922, *Dinter* 4734 (missing).

Lectotype: Klinghardt Mountains, Sept. 1922, *Dinter* (B).

Trichocaulon cinereum Pillans, *S. African Gard. & Country Life* 18: 62 (1928, special reprint).

Type: South Africa, Cape, north part of Richtersveld, Oct. 1926, *Pillans* 578t (BOL).

Trichocaulon kubusense Nel, *Kakteenkunde* 1933: 70 (1933).

Type: South Africa, Cape, under bushes at altitude of 400 m, Kubus, Oct. 1930, *Herre* sub *SUG* 6007 (missing).

Trichocaulon truncatum Pillans in A.C. White & B. Sloane, *Stap.*, ed. 2, 3:1029, fig. 1096 (1937).

Type: South Africa, Uroanop on Goodhouse road, *Smithers* sub BOL 21725 (BOL).

Included in the present concept of *L. perlata* are Figs. 1092-1096, 1112 (right hand only) and 1117 of White & Sloane (1937).

Shrublet branching from base, with 1-10 stems. Stems 50-300 mm long, 25-60 mm thick, erect, cylindrical clavate; *tubercles* flattened rounded polygonal, arranged into 12-14 rows along stem, each with small conical to flattened persistent leaf-rudiment < 1 mm long. *Inflorescences* mainly in upper parts of stem, flowers in groups of 3-6 (-12) on often large 'peduncular patches', opening in rapid succession (often several per cluster open at once), with strong excrement odour; *pedicel* 0.5-2.0 mm long, 1 mm thick; *sepals* 1.0-1.5 mm long, 0.5-1.0 mm broad at base, ovate, acute, margins usually ciliate with transparent thick hairs, otherwise glabrous. *Corolla* (5-) 7-10 mm diam., rotate; outside yellow-green; inside grey to greenish white to grey spotted with deep maroon to entirely deep maroon, covered densely with obtuse conical papillae each tipped with a horizontally spreading cylindrical obtuse bristle; *tube* 1.0-1.5 mm deep, shallowly cupular, containing gynostegium up to level of bases of inner lobes, not thickened at mouth; *lobes* 3.0-4.5 mm long, 2.0-2.5 mm broad at base, strongly reflexed and pressed against stem with bases raised into 'annulus' around mouth of tube, often with paler slightly raised medial ridge, narrowly ovate-deltate, acuminate, margins folded back strongly so inside convex. *Corona* ± 2.5 mm

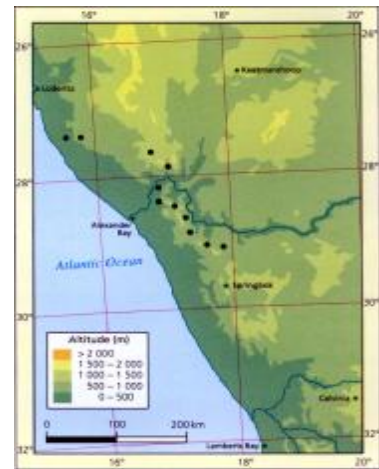


Fig. 6.12. Distribution of *Larryleachia perlata*.

tall, 2.0-3.5 mm broad, irregularly red- to maroon-spotted on yellow to whitish background, $\pm$ sessile; *outer lobes* ± 1 mm long, ascending, bifid to near middle into divergent spreading dorsiventrally flattened lobules up to 0.5 mm long or emarginate and truncate, laterally fused in lower half to bases of inner lobes to form pouch; *inner*

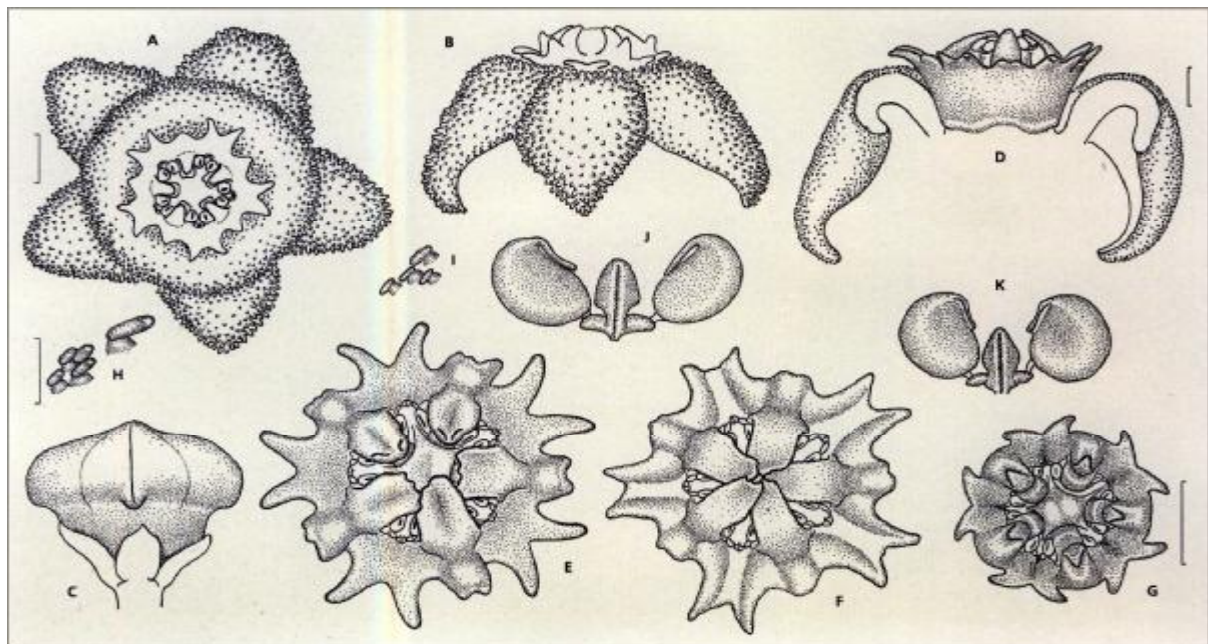


Fig. 6.13. *Larryleachia perlata*. A, face view of flower. B, side view of flower. C, bud. D, side view of dissected flower. E-G, face view of gynostegium. H, I, papillae inside corolla near base of lobes, apical appendage pointing towards tip of lobe. J, K, pollinarium. Scale bars: A, B, 1 mm (at A); C, D, 1 mm (at D); E-G, 1 mm (at G); H, I, 0.5 mm (at H); J, K, 0.25 mm (at H). Drawn from: A, B, H, cultivated material ZSS; C, E, J, *PVB* 3229 b, Rosyntjie Mountain; D, F, I, K, *Russel*, Cornellskop; G, *hort.* NBG, Richtersveld.



Fig. 6.14. *L. perlata*, PVB 8368, east of Lorelei, Namibia, plants with particularly small flowers.

/lobes $\pm$ 0.5 mm long, adpressed to backs of anthers and sometimes exceeding them, occasionally with erect apices, deltoid to rectangular, acute to truncate or emarginate, with broad truncate nearly erect dorsal projection at base in series with outer lobes.

Distribution and habitat

Larriyleachia perlata appears to occur in two disjunct areas. The larger of these areas begins in the mountains west and east of Rosh Pinah in southern Namibia and continues southwards across the Orange River to Sendeling's Drift and around Kubus. Plants are also found eastwards to Vioolsdrift and near Goodhouse and as far as the dry valley of the Wyepoort River a little north of Steinkopf. The other, very much smaller area appears to be isolated from the main body of the distribution and lies in the Klinghardt Mountains in the coastal Namib Desert about 100 km south of Lüderitz.

Specimens of *L. perlata* may be found in quartz patches. Plants are often found at lower altitudes in the Richtersveld on the lower slopes of hills growing wedged between rocks or emerging from a small crevice in an outcrop of schist or gneiss, fully in the open.

Diagnostic features and relationships

Although some plants of *L. perlata* may be small, stems of this species may reach a length of 300 mm. Plants consisting of 3-8 such stems from quite an impressive shrublet. Such large specimens have been seen in several places, especially around Hellskloof, the lower slopes of the Rosyntjie Mountain and east of Eksteenfontein.

In *L. perlata* the flowers arise in larger clusters than in the other species. The 'peduncular patches' from which they develop may become very large indeed (10 mm or more in diameter) and often will have one or more knobbly, scarred 'peduncles' projecting for up to 3-4 mm from it. More than one flower will often develop concurrently on each patch and often whole clusters open nearly together. This is not known in any other species of *Larriyleachia*.

The flowers of *L. perlata* are remarkably



Fig. 6.15. *L. perlata*, PVB 4648, east of Eksteenfontein.

variable in colour. They may be a uniform greyish yellow, almost cream to grey-pink to more or less densely spotted with deep maroon. In spotted flowers the spots are often missing in a line down the middle of each lobe and on the 'annulus'. Occasionally, uniformly deep maroon flowers are found. They are also variable in size



Fig. 6.16. *L. perlata*, PVB 3942, south of Remhoogte, Richtersveld.

and plants bearing flowers only 5 mm across may be encountered, though usually they are 7-10 mm in diameter. Small-flowered plants seem to be most typical of the arid country close to the Orange River and occur on both its southern and northern banks. Despite all this variability they have a very distinctive

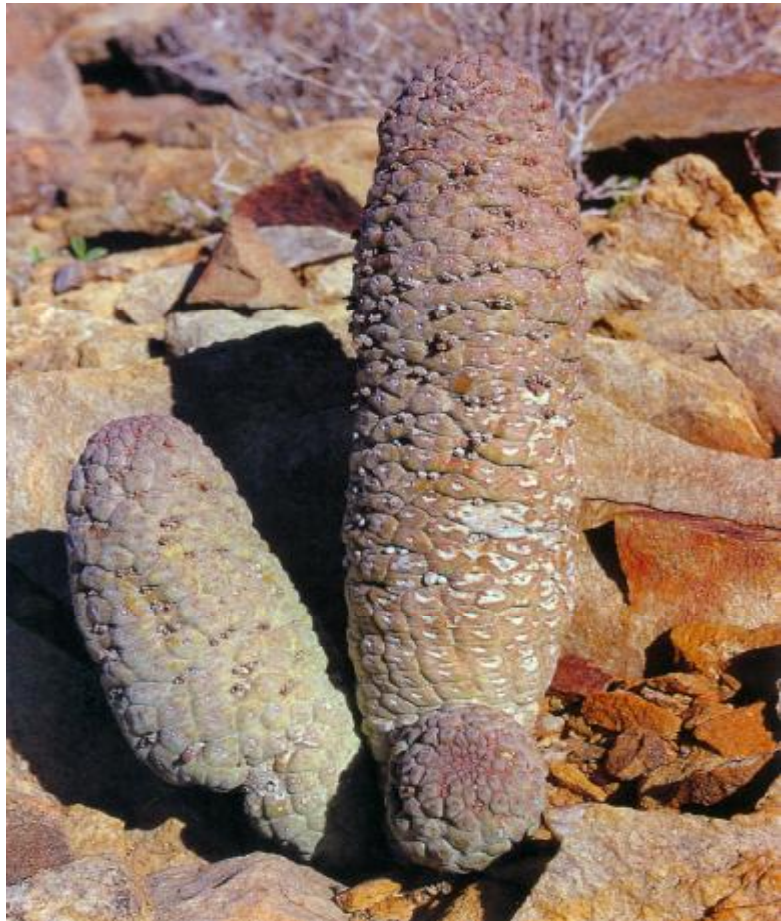


Fig. 6.17. *L. perlata*, PVB 4648, east of Eksteenfontein, July 1991.

LARRYLEACHIA CACTIFORMIS

shape and indumentum. The corolla lobes are always convex, with the margins usually quite strongly folded back, and quite often they have a raised, medial ridge along them. Just outside the mouth of the tube, the lobes are bent backwards and often pressed against the stem. This bending backwards gives rise to what appears to be an annulus around the mouth of the tube and surrounding the corona. However, unlike the annulus of *Hoodia pilifera*, for example, here there is no thickening of the tissue in this area and this is another case of a false annulus, as in some species of *Huernia*. The surface of the flower is quite obviously papillate inside. Under the microscope it can be seen that each of these papillae is small, roughly conical and tipped by a cylindrical bristle. These bristles have a unique shape, as each is rounded at both the front and the rear and lies horizontally on top of the papilla, facing the perimeter of the flower.

The small corolla tube contains most of the gynostegium. The corona is somewhat variable in shape, especially in the extent to which the outer lobes are bifid. It always seems to be yellow, densely and irregularly spotted with red or maroon.

History

Larryleachia perlata seems to have been collected for the first time by M. Kurt Dinter in 1922 at various locations in the Klinghardt Mountains to the south of Lüderitz. Several other collections were made in the Richtersveld shortly after this and each one was described as a new species. Cole (1979) was unequivocal in deciding that all these names applied to one variable species and no evidence has arisen to shake this conviction.



Fig. 6.18. *L. perlata*, Heunis, Namuskluft, Namibia.



Fig. 6.19. *L. perlata*, PVB 3942, south of Remhoogte, Richtersveld.

3. *Larryleachia cactiformis*

Larryleachia cactiformis (Hook.) Plowes, *Excelsa* 17: 5 (1996).

Stapelia cactiformis Hook., *Bot. Mag.* 70: t. 4127 (1844).

Trichocaulon cactiforme (Hook.) N.E.Br., *Hooker's Icon. Pl.* 20:t.1905 (1890), as '*cactiformis*'.

Leachia cactiformis (Hook.) Plowes, *Asklepios* 56:12 (1992).

Leachiella cactiformis (Hook.) Plowes, *Asklepios* 57: 15 (1992).

Lavrania cactiformis (Hook.) Bruyns, *S. African J. Bot.* 59: 342 (1993).

Hoodia cactiformis (Hook.) Halda, *Acta Mus. Richnov. Sect. Natur.* 5: 31 (1998).

Type: Little Namaqualand, Zeyher, fl. Aug. 1844 (missing).

Lectotype: *Bot. Mag.* 70: t. 4127.

Included in the present concept of *L. cactiformis* are Figs. 1098, 1102, 1103 of White & Sloane (1937).

Dwarf shrublet, branching from base, with 1-10 stems. Stems 40-150 (-200) mm long, 30-60 mm thick, erect, cylindrical clavate, whitish to grey-green; *tubercles* flattened rounded polygonal, crowded but arranged into $\pm$ 12-16 rows along stem, each tipped with small conical to flattened leaf-rudiment < 1 mm long. *Inflorescences* mainly near apex of stem, flowers arising in groups of 1-5, developing successively; *pedicel* 1-2 mm long, 1 mm thick; *sepals* $\pm$ 1.5 mm long, 1.0 mm broad at base, ovate, acute, glabrous except for cilia sometimes on margins. *Corolla* 6-15 mm diam., campanulate to shallowly campanulate; inside white to pale yellow barred (rarely spotted) with purple-red to $\pm$ uniformly purple-red or maroon, covered with obtuse papillae usually each with a small apical bristle; tube 1-3 mm deep, shallowly bowl-shaped.

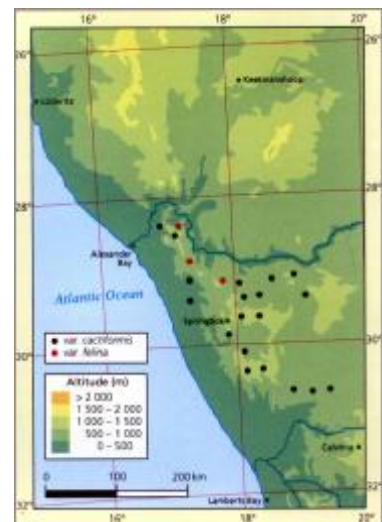


Fig. 6.20. Distribution of *Larryleachia cactiformis*.

to cupular, containing most of gynostegium; lobes 2.0-3.5 mm long, 2.5-5.5 mm broad at base, spreading, usually with recurved tips, broadly ovate-deltate, broadly acute, margins slightly recurved. Corona ± 1.5 mm tall, 3.0-4.5 mm broad, spotted and lined with red on yellowish background, $\pm$ sessile; outer lobes ± 1.5 mm long, ascending, bifid to well below middle into spreading-erect straight to slightly diverging slightly flattened obtuse lobules, laterally fused in lower half to bases of inner lobes; inner lobes ± 1.5 mm long, adpressed to backs of anthers and usually not exceeding them (sometimes meeting in centre and slightly overlapping), linear to narrowly deltoid, acute to truncate-emarginate, with $\pm$ deltoid erect to slightly spreading dorsal projection near base $\pm$ in series with outer lobes, usually white above with red margins.

Larryleachia cactiformis is less widespread than most of its congeners. It occurs over most of Namaqualand from near Sendelingsdrift to south of Port Nolloth on the coastal plain. Further east it occurs sporadically in the Kamiesberg and other mountains of Namaqualand, from Steinkopf to as far south as near Garies. It is quite common on many of the quartz hills of western Bushmanland, from east of Springbok to Aggeneys and Pofadder. *Larryleachia cactiformis* does not appear to grow in Namibia.



Fig. 6.21. *L. cactiformis* var. *cactiformis*, Heunis 11, north-west of Loeriesfontein.

Key to the varieties of *L. cactiformis*

Corolla 6-8 mm diam., inside at most faintly marked with pale yellow on purple-red to maroon	3a. var. <i>felina</i>
Corolla 10-15 mm diam., inside quite prominently transversely marked with purple-red on pale yellow	3b. var. <i>cactiformis</i>

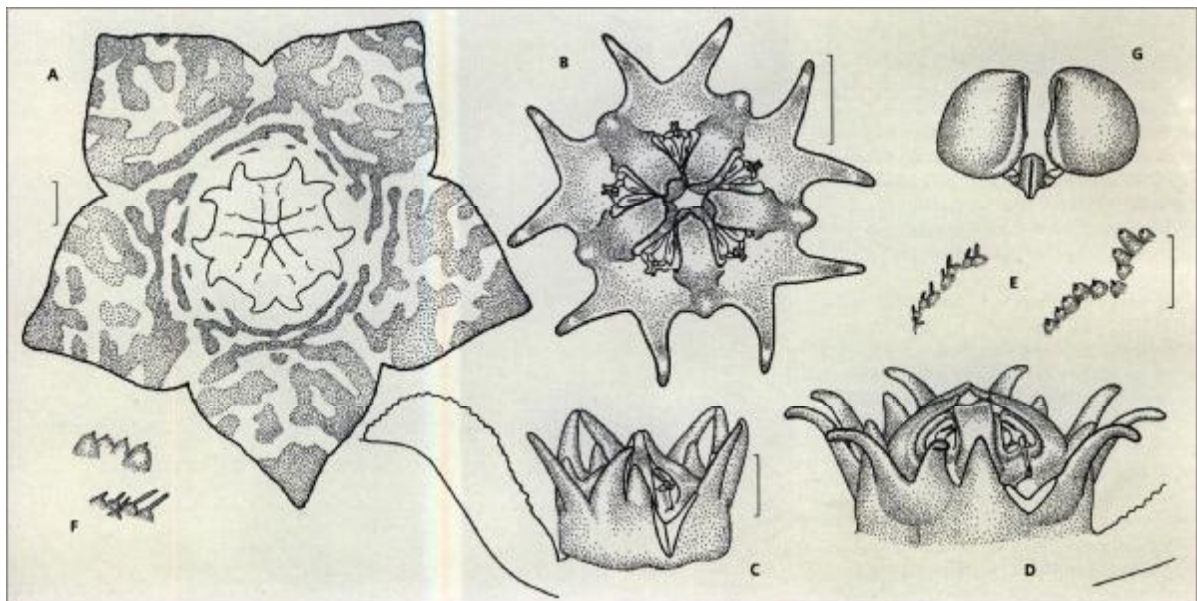


Fig. 6.22. *Larryleachia cactiformis* var. *cactiformis*. A, face view of flower. B, face view of gynostegium. C, D, side view of gynostegium. E, F, papillae inside corolla: with longer bristles from near tips of lobes; others near mouth of tube. G, pollinarium. Scale bars: A, 1 mm; B, D, 1 mm (at B); C, 1 mm; E, F, 0.5 mm (at E); G, 0.25 mm (at E). Drawn from: A, F, Heunis 11, north-west of Loeriesfontein; B, D, E, G, Kennedy, Kweekfontein; C, Heunis 112, east of Kamieskroon.

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3a. *Larryleachia cactiformis* var. *cactiformis*

Trichocaulon simile N.E.Br., Fl Cap. 4 (1): 895 (1909).

Leachia similis (N.E.Br.) Plowes, *Asklepios* 56:14 (1992).

Leachiella similis (N.E.Br.) Plowes, *Asklepios* 57:16 (1992).

Larryleachia similis (N.E.Br.) Plowes, *Excelsa* 17:12 (1996).

Hoodia similis (N.E.Br.) Halda, *Acta Mus. Richnov. Sect. Natur.* 5: 32 (1998).

Type: South Africa, near Vanrhynsdorp, Marloth 4571 (K).

Corolla shallowly campanulate, (8-) 10-15 mm diam.; inside white to pale yellow transversely barred (rarely spotted) with purple-red.

Distribution and habitat

Var. *cactiformis* is distributed over the whole area for the species.

Specimens of var. *cactiformis* are found in many different types of habitat. On the coastal plain plants often occur on the lower slopes of quartzite hills in bare places among stones or under small bushes. In the Kamiesberg it grows among small bushes on dry slopes and will even be found quite high up on gneiss domes in shallow pockets of soil with clumps of *Polymita albiflora* and species of *Conophytum*. On the quartz hills of Bushmanland it usually grows among stones on the lower slopes or in crevices between rocks high up.

Diagnostic features and relationships

Plants of var. *cactiformis* may be quite large and specimens with up to eight or 10 stems have been seen, though most of them have between one and three stems. Individual stems vary very much in size and have been seen on occasion up to 200 mm tall, though this is exceptional and many are small and ellipsoidal. The stems are sometimes spotted with purple on a grey background and this colouring is particularly common in the Kamiesberg.

In var. *cactiformis* the flowers are quite broad and nearly rotate. The corolla is covered inside with transverse bands of red or brown which generally tend to become finer towards the centre. The interior is covered with papillae which are comparatively large, though they are only clearly visible under a microscope.

The centre of the flower possesses a shallowly bowl-shaped tube which contains the entire gynostegium. This structure consists of ascending, deeply bifid outer lobes which are lined with red especially towards their apices. It also has small inner lobes which are as long as or slightly longer than the anthers but do not rise up significantly in the centre. They are often white with red margins.

Var. *cactiformis* is quite similar to *L. picta* and the two occur together at several localities to the west and south-west of Pofadder. There are several weak characters by which they may be separated: in *L. picta* the flower is larger with small, nearly circular, purple-brown spots on pale yellow (usually the corolla has elongated, transverse bands of red or brown on a whitish background in *L. cactiformis*); in *L. picta* the corolla tube is usually quite clearly pentagonal

(circular in *L. cactiformis*) and it has a shallower, broader gynostegium with more widely divergent outer corona lobes and a longer dorsal projection on the inner lobes than in *L. cactiformis*; in *L. picta* the papillae on the inside of the corolla are also usually more flattened and rarely have an apical bristle, while they are taller with sometimes quite long apical bristles in *L. cactiformis*.

The two taxa are most reliably distinguished



Fig. 6.23. *L. cactiformis* var. *cactiformis*, PVB 5340, near Paulshoek, Kamiesberg, a large specimen between gneiss rocks, September 1992.



Fig. 6.24. *L. cactiformis* var. *cactiformis*, PVB 4633, south-east of Port Nolloth, unusually darkly coloured flowers similar to some of var. *felina*.



Fig. 6.25. *L. cactiformis* var. *cactiformis*, Heunis 18, 30 km east of Springbok.



Fig. 6.26. *L. cactiformis* var. *cactiformis*, PVB 4633, south-east of Port Nolloth.

by the different inner corona lobes. In *L. cactiformis* these are incumbent on the backs of the anthers and mostly shorter than them but may exceed them slightly to meet in the centre. In one collection (east of Kamieskroon, Heunis 112) they were found to rise slightly in the centre but this is the only locality where this was seen. *Larryleachia cactiformis* is much less easily separated from *L. tirasmontana* and details of this are discussed under *L. tirasmontana*.

In the extreme north-west of the Northern Cape, from the Rosyntjie Mountain to just north of Steinkopf, an extraordinary range of variation can be found. Some of the more extreme of these plants from the Rosyntjie Mountain were given the name *Trichocaulon felinum* Cole. Although this name was not recognised in Bruyns (1993), it is felt that these plants are sufficiently distinctive to warrant some taxonomic recognition. Since they are connected to 'normal' *L. cactiformis* with a range of intermediates and since they occur within the distribution range of the remainder of *L. cactiformis*, they are given the rank of variety.

History

Larryleachia cactiformis was, in all probability, discovered by William Paterson as early as 1778, but it was definitely known to Zeyher from his trips to Namaqualand of 1829-31 and 1843. *Trichocaulon simile* was said to have been collected near Vanrhynsdorp and was found by Marloth around 1905. According to Brown's description (Brown 1907-09) the inner corona lobes shortly exceed the anthers and this suggests *T. cactiforme*. The type of this name is a single flower which proved to be of *T. cactiforme* (Bruyns 1993: 254) and so *T. simile* is a synonym of *L. cactiformis*. '*T. simile*' was figured in Phillips (1936) but this figure is of *L. picta*. This figure caused considerable confusion since it was reproduced uncritically in White & Sloane (1937), shaping, or perhaps muddling, their concept of this species and this error has been perpetuated in most of the recent popular literature (Plowes 1982; Cole 1979; 1984). The confusion between *L. cactiformis* and *L. picta* has persisted to the present day and the two species were muddled in Albers & Meve (2002).

3b. *Larryleachia cactiformis* var. *felina*

Larryleachia cactiformis var. *felina* (Cole)

Bruyns, comb. et stat. nov.

Trichocaulon felinum Cole, Aloe 22: 6 (1985).

Leachia felina (Cole) Plowes, Asklepios 56:12 (1992).

Leachiella felina (Cole) Plowes, Asklepios 57:16 (1992).

Larryleachia felina (Cole) Plowes, Exelsa 17: 7 (1996).

Hoodia felina (Cole) Halda, Acta Mus. Richnov. Sect.

Natur. 5: 31 (1998).

Type: South Africa, Richtersveld, near summit of Rosyntjie Mtn, July 1978, Cole CX 441 (PRE).

Included in the present concept of *L. cactiformis* var. *felina* is Plate XXXII c of Albers & Meve (2002).

Corolla campanulate, 6-8 mm diam.; inside uniformly purple-red to maroon, sometimes transversely barred with pale yellow to white.

Distribution and habitat

This variety occurs in the Richtersveld from the Rosyntjie Mtn to just north of Steinkopf and grows mainly on quartz outcrops.



Fig. 6.27. *L. cactiformis* var. *felina*, PVB 3229a, Rosyntjie Mountain.

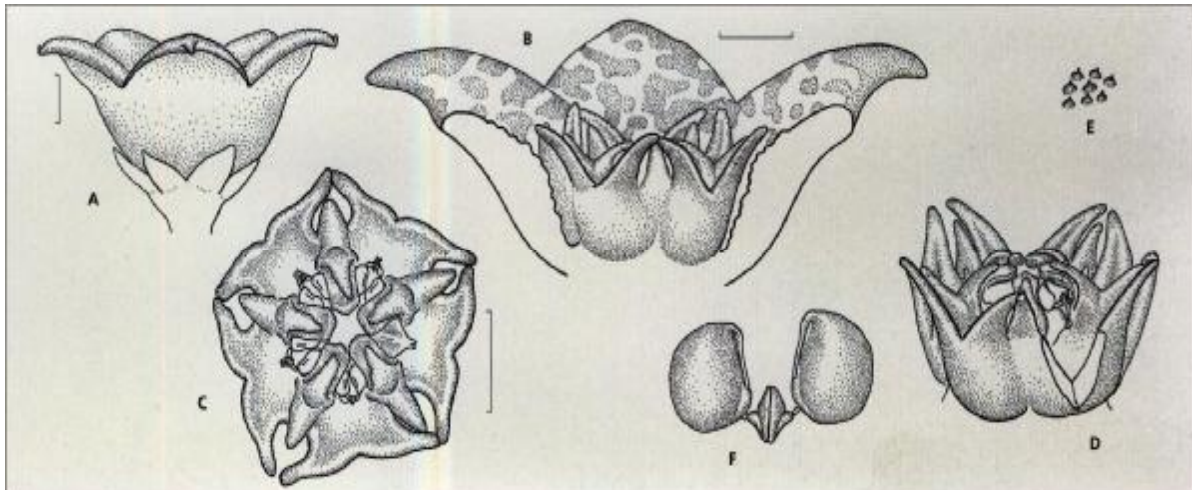


Fig. 6.28. *Larryleachia cactiformis* var. *felina*. A, side view of flower. B, side view of dissected flower. C, face view of gynostegium. D, side view of gynostegium with part of outer corona lobe removed. E, papillae inside corolla near base of lobes. F, pollinarium. Scale bars: A, 1 mm; B, 1 mm; C, D, 1 mm (at C); E, 0.5 mm (at B); F, 0.25 mm (at B). Drawn from: E, Cole 442, Rosyntjie Mountain; rest, PVB 3229a, Rosyntjie Mountain.

LARRYLEACHIA PICTA

Diagnostic features and relationships

In this variety the flowers are much smaller than in var. *cactiformis* and are often only 6 mm in diameter. They may also have very few small, pale transverse markings or none at all, so the corolla may be uniformly red to maroon. The flowers have a relatively deeper corolla tube and consequently the horns of the inner corona lobes rise more steeply. They are also sometimes less papillate than normal, with the papillae restricted to the tube. Differences in the corona between the two varieties are not always reliable, though the lobes are often shorter in var. *felina*, with the inner lobes usually narrower towards their apices.



Fig. 6.30. *L. cactiformis* var. *felina*, PVB 4649, east of Eksteenfontein.

History

Var. *felina* was discovered by Desmond T. Cole in July 1974 on the Rosyntjie Mountain in the northern Richtersveld.



Fig. 6.29. *L. cactiformis* var. *felina*, PVB 4649, east of Eksteenfontein.



Fig. 6.31. *L. cactiformis* var. *felina*, Heunis 119, north of Steinkopf.



Fig. 6.32. *L. cactiformis* var. *felina*, Heunis 118, north of Steinkopf.

4. *Larryleachia picta*

Larryleachia picta (N.E.Br.) Plowes, *Excelsa* 17: 9 (1996).

Trichocaulon pictum N.E.Br., *Bull. Misc. Inform.* 1909: 307 (1909).

Leachia picta (N.E.Br.) Plowes, *Asklepios* 56:14 (1992).

Leachiella picta (N.E.Br.) Plowes, *Asklepios* 57:16 (1992).

Lawrania picta (N.E.Br.) Bruyns, *S. African J. Bot.* 59: 342 (1993).

Hoodia picta (N.E.Br.) Halda, *Acta Mus. Richnov. Sect. Natur.* 5: 32 (1998).

Type: South Africa, Little Namaqualand, Marloth 4596 (missing).

Neotype: Fl. Pl. South Africa 16: t. 620 (1936).

Trichocaulon meloforme Marloth, *Trans. Roy. Soc. South Africa* 2: 239 (1912).

Leachia meloformis (Marloth) Plowes, *Asklepios* 56: 12 (1992).

Leachiella meloformis (Marloth) Plowes, *Asklepios* 57: 16 (1992).

Larryleachia meloformis (Marloth) Plowes, *Excelsa* 17: 7 (1996).

Hoodia meloformis (Marloth) Halda, *Acta Mus. Richnov. Sect. Natur.* 5: 32 (1998).

Type: Namibia between granite boulders near Aus, 1400 m, Marloth 4874 (PRE).

Trichocaulon engleri Dinter, *Neue Pflanzen Deutsch-SWA*: 56 (1914).

Type: Namibia, Us Tal, nord-östlich von Kanus, Engler 3083 = Dinter 3136 (SAM).

Included in the present concept of *L. picta* are Figs. 1062, 1099, 1100, 1104, 1105, 1106, 1114 of White & Sloane (1937) and Plate XXXIIb of Albers & Meve (2002).

Dwarf shrublet, rarely branching from base, with 1-5 stems. Stems 30-200 mm long, 20-60 mm thick, erect, cylindrical clavate or $\pm$ spherical, whitish to grey-green; *tubercles* flattened rounded polygonal, crowded but arranged into $\pm$ 12-16 rows along stem, each tipped with small conical to flattened leaf-rudiment < 1 mm long. *Inflorescences* mainly near apex of stem, flowers arising in groups of 1-5, developing successively; *pedicel* 0.5-1.5 mm long, 1.0 mm thick; *sepals* 2 mm long, 1 mm broad at base, lanceolate-ovate, acute, keeled towards

apex, glabrous. *Corolla* 8-16 mm diam., shallowly campanulate; inside with purple to red spots on white to pale yellow background and usually with purple-brown patch on apex of lobes, covered with dome-shaped papillae each with or without short apical bristle; *tube* ± 2 mm deep, cupular, pentagonal with inward-pointing bulges opposite anthers; *lobes* 2-3 mm long, 3-5 mm broad at base, spreading with strongly reflexed tips, ovate-deltate, acute, margins slightly recurved. *Corona* ± 2.5 mm tall, 5-6 mm broad, whitish spotted with purple-black, raised on very short stipe; *outer lobes* 1.5-2.5 mm long, spreading, bifid almost to base into widely divergent spreading slightly dorsiventrally flattened lobules, laterally fused near base to bases of inner lobes into shallow pouch; *inner lobes* 2.0-2.5 mm long, adpressed to backs of anthers and exceeding them then connivent-erect and rising into column in centre, linear, obtuse, with spreading narrowly conical dorsal projection ± 1.5 mm long near base arising inside but confluent with outer lobes.

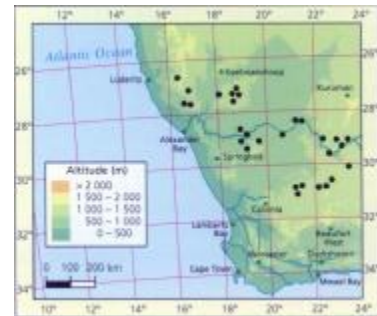


Fig. 6.33. Distribution of *Larryleachia picta*.

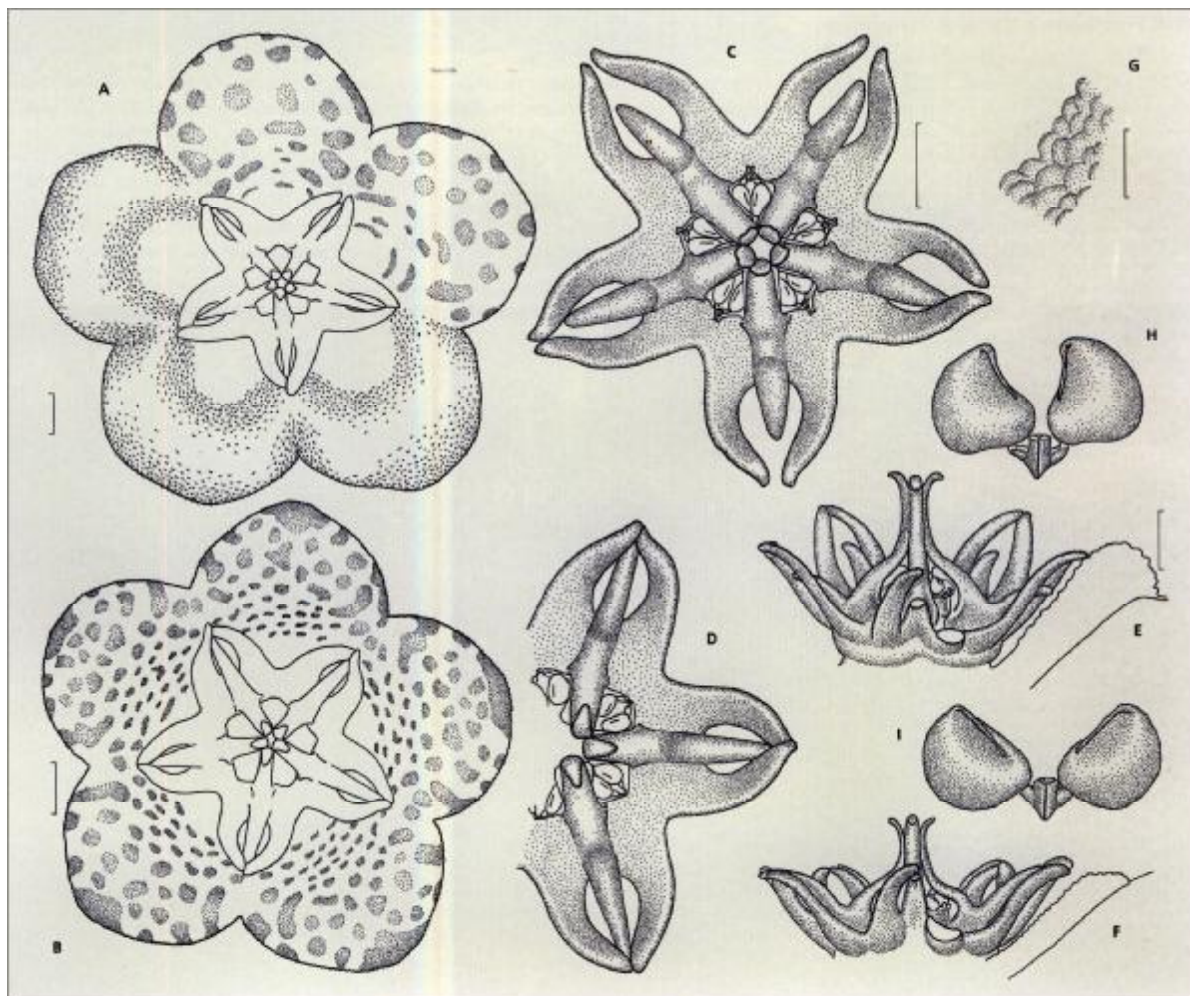


Fig. 6.34. *Larryleachia picta*. A, B, face view of flower. C, D, face view of gynostegium. E, F, side view of gynostegium. G, papillae inside corolla tube. H, I, pollinarium. Scale bars: A, B, 1 mm; C, D, 1 mm (at C); E, F, 1 mm (at E); G, 0.5 mm; H, I, 0.25 mm (at G). Drawn from: A, C, E, G, H, *Heunis* 3, just north of Aus, Namibia; B, D, F, I, *PVB* 3747, north-west of Carnarvon.

LARRYLEACHIA PICTA

Distribution and habitat

Larryleachia picta grows along the eastern edge of the winter-rainfall region from Aus to Witpütz in south-western Namibia, via the Great Karas Mountains to as far east as Douglas in Griqualand West in South Africa and then southwards to Williston, Carnarvon and Strydenburg. There do not seem to be any records at all for Namaqualand.

Plants of *L. picta* are sometimes found in flattish quartz patches (e.g. around Witpütz and Pofadder) but are more usually encountered in populations of very scattered individuals among rocks (dolerite, granite, calcrete or various shales) from around the base to the tops of hills and to altitudes of 1 600 m or more in the Great Karas Mountains.

Diagnostic features and relationships

Flowers of *L. picta* are generally large for this genus. On the background colour there are numerous, nearly round, evenly distributed, purple-brown spots which often become somewhat transversely elongated in the tube. This patterning extends along the lobe for most of its length except near the apex, which is usually dark purple-brown. However, the apex of the lobe is mostly folded back once the flower



Fig. 6.35. *L. picta*, PVB 3904, mountains east of Witpütz, Namibia.

is fully open, making this dark patch visible only as the flowers open. The corolla tube has a broad inward bulge at the sinuses of the lobes and this gives the tube a distinctly pentagonal shape that is rarely found in *L. cactiformis*. As is common in the genus, the inside of the corolla is covered with papillae but here they are broad and rounded, often with a dark, apical cell and only rarely with an apical bristle.

The corona is particularly variable. Usually the horns of the outer lobes are divergent and spreading so as to lie close to (sometimes adpressed to or curling round) the long dorsal projection of the inner lobe. As a consequence the outer series has the appearance of being made up of five trifid lobes; occasionally they do not diverge at all and the 15 horns (10 outer



Fig. 6.36. *L. picta*, Heunis & Bruyns 27, north of Witpütz, Namibia.

coronal horns and five dorsal projections on the inner lobes) are more or less equally spaced. In *L. picta* the inner lobes are relatively long. They are initially incumbent on the anthers, then connivent and then erect, rising in a slender vertical column above the centre of the flower and exceeding the height of the outer lobes. In a few cases they have been found to form a cage above the anthers. In such flowers they are incumbent on the anthers only near their bases, after which they rise above them and meet in the centre to form a small vertical column.

It has been found that in *L. cactiformis* and *L. picta* the seed and seedlings are markedly different, whereas their vegetative and floral parts are somewhat similar and the two species could be confused. Florally they are most



Fig. 6.37. *L. picta*, PVB 5766, western summits of the Great Karas Mountains, Namibia, a medium-sized plant consisting of a single stem, growing at the base of a driedoring (*Rhigozum trichotomum*), March 1993.



Fig. 6.38. *L. picta*, PVB 7557, north of Williston.

readily separable by the long inner corona lobes of *L. picta*. There are other less reliable distinctions, and these are discussed under *L. cactiformis*.

History

The type of *L. picta* was discovered by Rudolf Marloth in about 1908 somewhere in Namaqualand. Since there have been problems with the application of this name, a careful investigation of the relevant descriptions and of several types and other important specimens was carried out and this was reported in Bruyns (1993). The



Fig. 6.39. *L. picta*, Heunis 3, just north of Aus, Namibia.

type of *Trichocaulon pictum* is missing. In his description N.E. Brown referred to the inner corona lobes as 'exceeding the anthers with the apices connivent-erect' and this is true of the figure that he later published (Brown 1914). This figure was supposed to have been based on a specimen of Pearson's from Chubiesies in the Richtersveld [Pearson 6192] but it was found that this specimen did not have the inner corona lobes exceeding the anthers and therefore belonged to *T. cactiforme* (this being the main character on which the two species can be separated and is quite obvious in pressed material). It follows that the specimen Pearson 6192 and the supposed figure of it (Brown 1914) do not represent the same species and it remains unclear from exactly which specimen this figure was prepared. So as to avoid any further confusion with this figure and the specimen Pearson 6192 of *T. cactiforme*, I selected an entirely different figure which also satisfies the description of N.E. Brown (1907-09) as the neotype (Bruyns 1993).

Plowes (1978a) suggested that all the names which are spread here under *L. cactiformis* and *L. picta* were synonyms of *L. cactiformis*. Cole (1979) took material from the Chubiesies area to represent *T. pictum* and, since this seemed to him to be quite clearly *T. cactiforme*, he suggested that *T. pictum* and *T. meloforme* were synonyms. He referred to the present species (with inner corona lobes exceeding the anthers and connivent-erect) as *Trichocaulon simile* and suggested that *T. engleri* and *T. cactiforme* were synonyms of this. Since the type of *T. simile* has proved to be a flower of *T. cactiforme* (Bruyns 1993), this is not the correct synonymy and *T. engleri* and *T. meloforme* are both synonyms of *T. pictum*.

5. *Larryleachia tirasmontana*

Larryleachia tirasmontana (Plowes) Plowes, *Excelsa* 17:15 (1996).

Leachiella tirasmontana Plowes, *Brit. Cact. Succ. J.* 11:58(1993).

Hoodia tirasmontana (Plowes) Halda, *Acta Mus. Richnov. Sect. Natur.* 5: 32 (1998).

Type: Namibia, Tiras Mountains, Plowes 4306 (SRGH).

Lavrania picta subsp. *parvipunctata* Bruyns, *Bot. Jahrb. Syst.* 115: 256 (1993).

Type: Namibia, Tiras Mountains, Heunis 6 (BOL).

Dwarf shrublet mostly with single stem. Stem 30-180 mm long, 20-50 mm thick, erect, clavate, whitish to grey-green; tubercles flattened rounded polygonal, crowded but arranged into $\pm$ 12-16 rows along stem, each tipped with small conical to flattened leaf-remnant < 1mm long. Inflorescences mainly near apex of stem, flowers arising in groups of 1-5, developing successively; pedicels 0.5-1.0 mm long, 1 mm thick; sepals 2 mm long, 1 mm broad at base, lanceolate-ovate, acute, keeled towards apex, glabrous, pale green faintly suffused with red. Corolla 8-9 mm diam., shallowly campanulate; outside greenish spotted with red; inside with dome-shaped papillae each with minute apical bristle, cream finely spotted with red and with dark red area near apex of each lobe; tube $\pm$ 2 mm deep, cupular, pentagonal; lobes 2 mm long, 3 mm broad at base, spreading, ovate-deltate, acute, margins slightly recurved. Corona $\pm$ 2 mm tall, 4 mm broad, pale yellow spotted with red, raised on very short stipe; outer lobes $\pm$ 1.5 mm long, ascending, bifid almost to base into widely divergent terete to flattened lobules usually with recurved tips; inner lobes $\pm$ 2 mm long, adpressed to backs of anthers and exceeding them then connivent-ascending in centre and rising together for $\pm$ 0.5 mm or less, with spreading conical dorsal projection < 1 mm long.

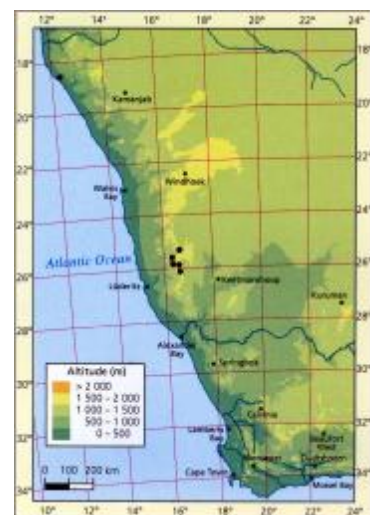


Fig. 6.40. Distribution of *Larryleachia tirasmontana*.

LARRYLEACHIA TIRASMONTANA

Distribution and habitat

Larryleachia tirasmontana has proved to be far more widespread than was previously realised (Bruyns 1993). It is of scattered occurrence around the base of and within the Tiras Mountains, beginning some 70 km north of Aus in southern Namibia. Further records exist from the Rooiberg, south-west of Maltahöhe, and at Tsamis West in the Naukluft (Plowes 1982: 21). The most remarkable northward extension of its known range is provided by material collected in December 1999 along the edge of the Skeleton Coast Park south-west of Orupembe and only about 150 km south of the Kunene River.

Larryleachia tirasmontana grows between stones or under short bushes on granitic hillsides at altitudes between 350 m (on the Skeleton Coast) and 1 950 m in the Tiras Mountains.



Fig. 6.43. *L. tirasmontana*, PVB 5689, west of Helmeringhausen, Namibia.



Fig. 6.41. *L. tirasmontana*, Heunis 6, Tiras Mountains, south of Helmeringhausen, Namibia.



Fig. 6.42. *L. tirasmontana*, PVB 8066, south-west of Orupembe, Skeleton Coast, Namibia.

Diagnostic features and relationships

In the wild, plants of *L. tirasmontana* mostly consist of only one unbranched stem. Occasionally a very large specimen up to 180 mm tall and 50 mm thick may be found, but most are less than 80 mm tall. They seem to reach maturity quickly and often individuals only 50 mm high are found to be covered on top with flowers.

In this species the flowers are smaller than those of *L. picta* and the corolla is cream and very finely spotted with red. The tips of the corolla lobes are also red. Apart from this difference in colour between the two species, the inner corona lobes are shorter and connivent-ascending in the centre rather than connivent-erect into a small column.

In respect of the inner corona lobes, *L. tirasmontana* is strongly suggestive of *L. cactiformis*. It has, however, the long, widely diverging outer coronal horns typical of *L. picta*. The inner corona lobes rise slightly in the centre (more so than is usual for *L. cactiformis*) and they have a more spreading dorsal horn than

is usual in *L. cactiformis*, where it is normally erect. This dorsal horn is, however, not as long as it usually is in *L. picta*. The fine spotting of the corolla with red is more typical of *L. picta* than of *L. cactiformis*, where the dark colour is distributed mostly in transverse bars against the pale background. The seed and seedlings are indistinguishable from those of *L. picta* but are not at all similar to those of *L. cactiformis*.

History

Larryleachia tirasmontana appears to have been collected first in the Naukluft in Namibia by a Mrs. Kowie Archer (Plowes 1993). In Plowes (1982) it was said 'to be preferable to *T. cactiforme*' and it was figured under the name *Leachia cactiformis* in Plowes (1992). Although *L. cactiformis* and *L. tirasmontana* are not easy to separate, morphological features such as the manner in which the corolla is spotted, the length of the corona lobes and, most importantly, characters of the seed and seedling, all point to *L. tirasmontana* being closest to *L. picta*.

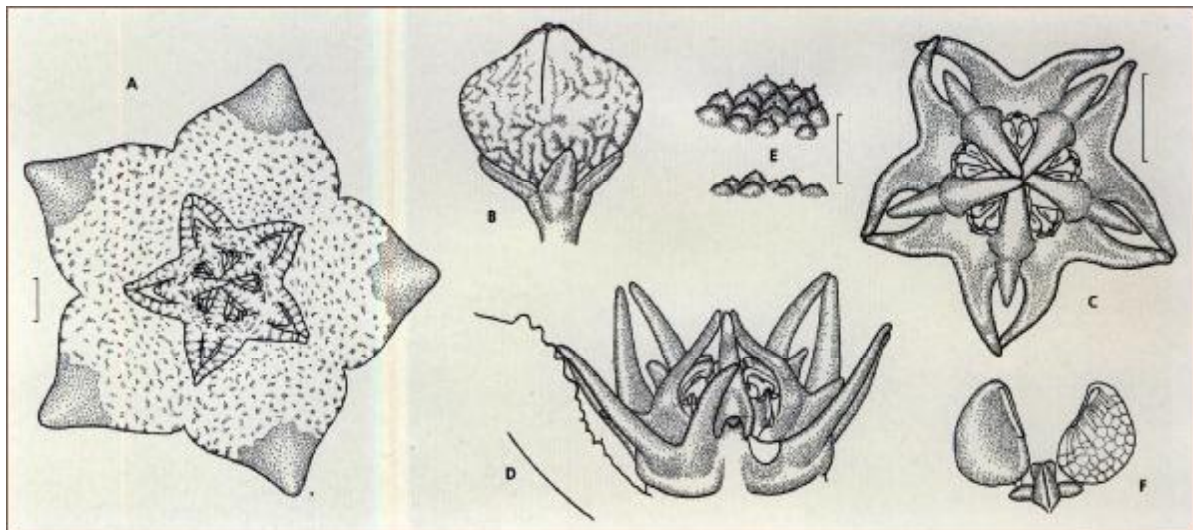
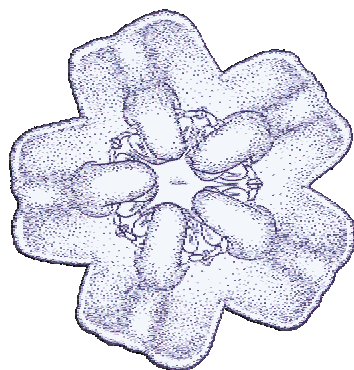


Fig. 6.44. *Larryleachia tirasmontana*. A, face view of flower. B, bud. C, face view of gynostegium. D, side view of gynostegium. E, papillae inside corolla: upper from tube, lower from base of lobes. F, pollinarium. Scale bars: A, B, 1 mm (at A); C, D, 1 mm (at C); E, 0.5 mm; F, 0.25 mm (at E). Drawn from: A, B, E, PVB 4173, Rooiberg Suid, south-west of Maltahöhe, Namibia; rest, PVB 3750, Tiras, Namibia.

7. Lavrania



Lavrania Plowes, Cact. Succ. J. (US) 58:122 (1986).
Hoodia subgen. *Lavrania* (Plowes) Halda, Acta Mus.
 Richnov. Sect. Natur. 5: 30 (1998).
Hoodia sect. *Lavrania* (Plowes) Halda, Acta Mus.
 Richnov. Sect. Natur. 5: 32 (1998).
 Type: *Lavrania haagnerae* Plowes.

The monotypic *Lavrania* was described in 1986. On this occasion (Plowes 1986) two main features distinguishing this new genus from the spineless species of *Trichocaulon* (now in *Laryleachia*) were given: (1) the more or less basally produced flowers and (2) the uniqueness of the 'bristle-tipped papillae' on the face of the corolla.

In *L. haagnerae* flowers are mainly found in the lower half of the stem, though inflorescences may be found most of the way up a floriferous axis (Bruyns 1999c). In the five species of *Laryleachia* the inflorescences are very numerous and bear flowers immediately after they are produced so that flowers are mainly found in the upper half of the stem. Nevertheless, many of these inflorescences remain active for a long time, so flowers can actually be seen practically anywhere on the floriferous axis. The second criterion does not stand up to a critical examination at all and in Bruyns (1993) it was shown that similar papillae are also found in *Laryleachia cactiformis*, *L. picta* and *L. perlata*.

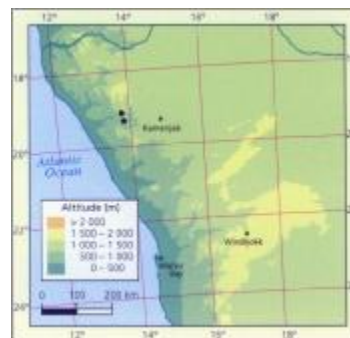


Fig. 7.1. Distribution of *Lavrania haagnerae*.

On account of this lack of clear morphological differences (other than the single, mainly basal inflorescence in *L. haagnerae* which leads to the long and uninterrupted rows of low tubercles) between these two groups of species, I placed all of them in the genus

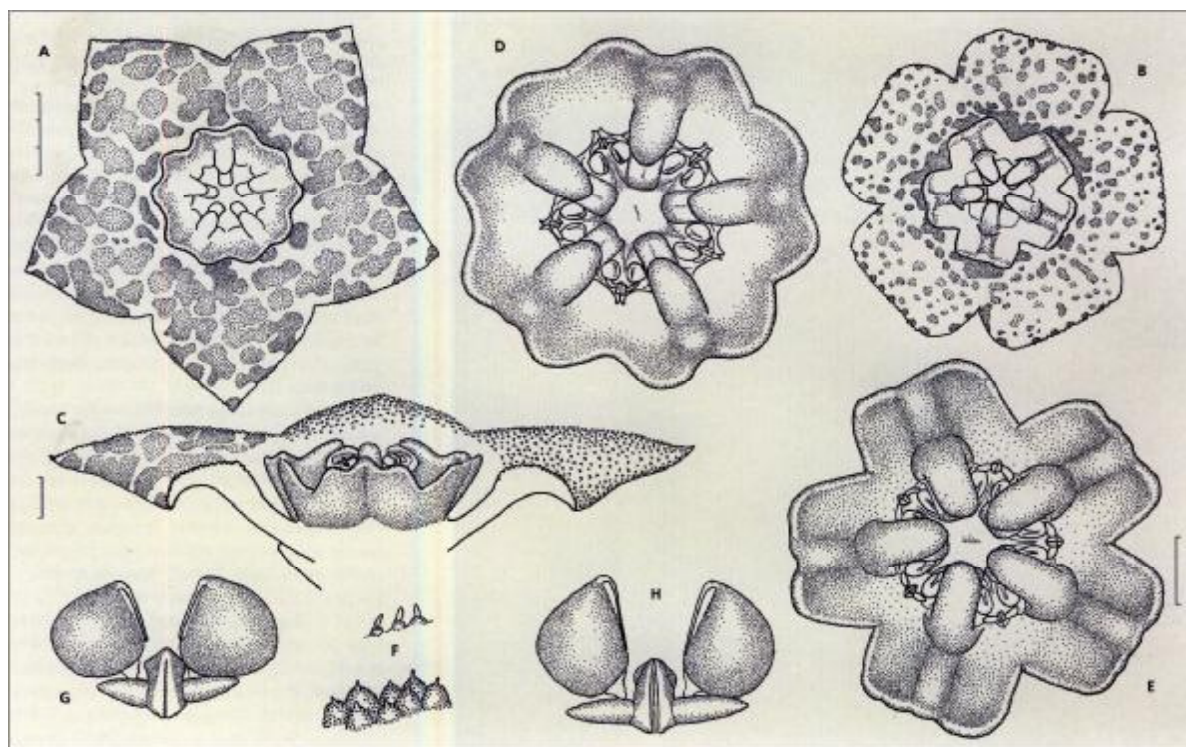


Fig. 7.2. *Lavrania haagnerae*. A, B, face view of flower. C, side view of dissected flower. D, E, face view of gynostegium. F, papillae on inside of corolla beyond tube. G, H, pollinarium. Scale bars: A, B, 3 mm (at A); C, 1 mm; D, E, 1 mm (at E); F, 0.5 mm (at E); G, H, 0.25 mm (at E). Drawn from: A, C, D, F, G, *Haagner sub* Plowes 5046, ? Khowarib gorge, Namibia; B, E, H, *PVB 4069*, near Sesfontein, Namibia.

LAVRANIA HAAGNERAE

Lavrania. However, Meve & Liede (2001b; 2002) have shown that this arrangement is not supported by molecular evidence. In both of these papers the statistical support for their groups is extremely low. Our own molecular research has yielded a similarly poorly supported and largely unresolved arrangement. This provides an interesting case where the morphological data suggests that two groups of species could be considered as one, and where the molecular data provide no significant help in making a decision. A strong argument for keeping them separate is that these are plants where many of the features are extremely reduced and that consequently the morphological data are misleading. However, on the other hand, recognising taxa for which there are no clear distinguishing morphological characters is risky. Nevertheless, for the time being two separate genera are recognised and *Lavrania* is restricted to the single species *L. haagnerae*.

Like *Hoodia* and *Larryleachia*, *Lavrania* is found only in arid situations and is associated with the Namib Desert. It is of very local occurrence in north-western Namibia.

Lavrania haagnerae

Lavrania haagnerae Plowes, *Cact. Succ. J. (US)* 58: 123 (1986).

Hoodia haagnerae (Plowes) Halda, *Acta Mus.*

Richnov. Sect. Natur. 5: 33 (1998).

Type: Namibia, Khawarib Gorge on Hoanib River south-east of Sesfontein, *Haagner sub Plowes* 5046 (PRE).

Spineless non-rhizomatous succulent forming shrublet consisting of cluster of 3-100 or more stems, branching mainly from base. Stems 60-300 mm long, 20-30 mm thick, decumbent to erect, cylindrical; *tubercles* flattened polygonal, arranged into 10-12 rows along stem, each tipped with small conical persistent leaf-rudiment < 1 mm long. *Inflorescences* 1-5 per stem mainly in lower half, each with 3-15 flowers arising on 'peduncular patches', opening in rapid succession; *pedicel* 2-12 mm long, 1-2 mm thick; *sepals* 2.5 mm long, 1.5 mm broad at base, ovate-deltate, acute. *Corolla* 13-16 mm diam, $\pm$ rotate; outside pale whitish green; inside spotted with red on yellow background, covered with obtuse papillae (except in tube) each tipped with a small obtuse to acute bristle; *tube* 1.0-1.5 mm deep, shallowly cup-shaped and just containing gynostegium, with corolla very slightly thickened at mouth; *lobes* 3-4 mm long, 6 mm broad at base, spreading, broadly ovate-deltate, broadly acute, margins slightly folded back. *Corona* $\pm$ 2 mm tall, 5 mm broad, pink-red, consisting of 2 series of lobes arising on staminal tube and partly intergrown, glabrous, sessile; *outer lobes* $\pm$ 1.5 mm long, ascending, bifid to middle into ascending very obtuse lobes laterally fused for nearly whole of length to dorsal projection of inner lobe, margins all somewhat rough; *inner lobes* < 1 mm long, adpressed to backs of anthers and shorter than them, linear, obtuse, with obtuse ascending dorsal projection confluent with and slightly taller than outer lobes.



Fig. 73. *L. haagnerae*, PVB 4069, near Sesfontein, Namibia, small plant after removal from ledge on cliff-face, January 1990.

Distribution and habitat

Lavrania haagnerae is found on the Damaraland-Kaokoveld border in the mountains around Sesfontein in north-western Namibia. It is now known from two localities dispersed over a distance of about 20 km and there are other precipitous spots in the area where it may also occur.

L. haagnerae occurs only on ledges on vertical, dolomitic cliffs which are inhabited by large quantities of *Aloe dewinteri* and very little other vegetation (figs. 57, 58). Like this aloe, the plants are of quite unbelievably difficult access and some rock-climbing skills are necessary to edge out on ledges and climb past overhangs to gain access to them. Plants are not uncommon and they form often quite large clumps in narrow crevices and small ledges on the rock faces. They are shallowly rooted in small pockets of soil and seem well able to spread along small veins of soil in the rock. This enables them to become quite large on occasion.

Diagnostic features and relationships

Plants of *L. haagnerae* form clumps which contain between three and 100 stems. Occasionally very large clumps have been observed and one about 150 mm broad and nearly 1 m long was noticed in January 1990. Mostly the stems are 60-100 mm long, but specimens where they reached 300 mm long have been seen in the wild.

The stems are covered with tubercles which are round, usually broader than tall and often somewhat polygonal in outline. They are only slightly joined together into longitudinal rows. Each tubercle has a rounded-truncate summit, usually with a shallow depression a little above the centre in which the minute leaf-rudiment is situated. *Lavrania haagnerae* has very oddly shaped leaf-rudiments, which are almost perfectly conical (fig. 17 B). They are persistent and remain soft.

The surface of the stem in *Lavrania* is papillate and many of the epidermal cells have their outer walls raised into a rounded papilla. The stomata are often deeply sunken between the other epidermal cells and they have unusual ridged sides to the pits in which they are seated (Bruyns 1993: fig. 5C). Such ridged pits are otherwise only known in some species of *Pectinaria*.

In *L. haagnerae* the primary stem does not bear flowers and inflorescences tend to arise in small numbers (up to 10 on each stem) towards the base of the secondary stems. As a consequence, the 10-12 rows of tubercles are very regular along most of the length of a floriferous stem. The inflorescences normally mature and bear flowers long after they are produced and thus flowers are mainly found in the lower half

of the stem. Nevertheless, occasional stems are found with flowers near their apex as well (Bruyns 1999c).

The flowers of *L. haagnerae* are more or less flat with a shallow, bowl-shaped tube in the centre and are very strikingly coloured. In the type the flowers had an intense and regular mottling of roundish red spots on a yellow background. Although such flowers have been seen in more recent collections, there are others in which the corolla is more finely spotted and sometimes the spots are so minute that the flower appears to be almost plain yellow dusted finely with red (fig. 7.5). They are densely covered on the inside with conical, obtuse papillae and give off an unusually strong odour that is reminiscent of rock-rabbit dung and urine.

The pinkish red corona fits almost exactly into the corolla tube so as to be more or less flush with the surface of the corolla. There is more or less no stipe beneath the gynostegium. The outer lobes form a broad cup. Each lobe is almost entire, often with a deeply triangular, medial notch and the edges of the outer lobes spread laterally to form a broad area behind each inner lobe. The inner lobes are small and pressed to the backs of the anthers. Both they and the margins of the outer lobes become covered with small, sweat-like drops of nectar.

History

This species was discovered fortuitously by Margaret Elliot 'Peggy' Haagner (née Kennedy, 1 April 1926-) in August 1969 during an expedition to Damaraland and the Kaokoveld. Mrs. Haagner found a piece of stem of *L. haagnerae* lying together with some dislodged plants of *Aloe dewinteri* at the foot of a series of enormous cliffs near the road east of Sesfontein. The species was described from material grown from this piece. It appears to have been assumed that this material was collected in the Khovarib Gorge and all attempts to relocate it there in habitat have failed (Plowes 1986). Plowes insisted that this place was the unique habitat for this plant but there is no evidence that it occurs there at all. Plants were eventually located in the wild early in January of 1990 at a different locality and it has been seen more recently probably more or less where Mrs. Haagner originally found it.

When it was first mentioned in the literature, *L. haagnerae* was quite categorically stated to be a new species of *Echidnopsis* (Plowes 1982) and the type specimen was labelled '*Echidnopsis namibensis*'. However, by the time it came to be published, it was described as the sole member of a new genus *Lavrania* (Plowes 1986).



Fig. 7.4. *L. haagnerae*, PVB 4069, near Sesfontein, Namibia, a plant with unusually darkly-coloured flowers.



Fig. 7.5. *L. haagnerae*, PVB 4069, near Sesfontein, Namibia.

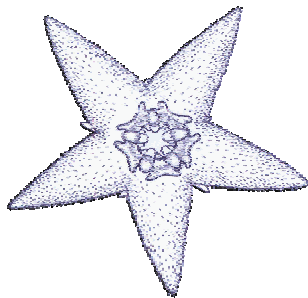


Fig. 7.6. *L. haagnerae*, PVB 4069, near Sesfontein, Namibia.



Fig. 7.7. *L. haagnerae*, PVB 4069, near Sesfontein, Namibia.

8. Notechidnopsis



Notechidnopsis Lavranos & Bleck, *Cact. Succ. J.*
(US) 57: 255 (1985).

Type: *Notechidnopsis tessellata* (Pillans) Lavranos &
Bleck.

Until 2002 this small genus contained two species, which have had a somewhat chequered taxonomic history. *Notechidnopsis tessellata* and its synonym *Echidnopsis*

serpentina were both initially described as species of *Caralluma*. They were then moved to *Echidnopsis* by White & Sloane (1937). The name *Echidnopsis tessellata* already existed (*E. tessellata* (Decne.) K. Schum. = (*E. cereiformis* Hook. f.) and hence the new name *E. framesii* was created to replace *Caralluma tessellata* Pillans. Finally, both *Echidnopsis serpentina* and *E. framesii* were placed under one name in *Notechidnopsis*.

Notechidnopsis columnaris was described as *Trichocaulon columnare* by G.C. Nel, who considered his species to represent a transitional phase between the two groups *Eutrichocaulon* and *Cactoidea* of *Trichocaulon*. Dyer and Hardy (1968) transferred this species to *Echidnopsis* but they did not explain why this was necessary.

In 1985 Lavranos & Bleck moved these two species out of *Echidnopsis* and established a new genus, *Notechidnopsis*, for them. A careful examination of characters in these two species (Bruyns 1999d) suggested that this arrangement is correct and that the

similar tessellate appearance of the stems in *Echidnopsis* and *Notechidnopsis* is a consequence of convergence and not of a close relationship between them. This examination revealed that *Notechidnopsis* is monophyletic and most closely related to *Pectinaria*. It was also shown that it shares many similarities with *Quaqua*. However, more recent molecular treatments (Meve & Liede 2002) have not supported all these conclusions. These studies have indeed confirmed that neither species is closely related to any in *Echidnopsis* but they also seem to indicate that *Notechidnopsis* is not monophyletic. Our own research shows that the two species formerly in *Notechidnopsis* appear to be more closely related to such genera as *Duvalia*, *Hoodia*, *Huernia*, *Lavrania*, *Orbea* and *Stapelia* than to *Pectinaria*, *Quaqua* and *Stapeliopsis*. The relationships between the two species remain more or less unresolved. Nevertheless, Meve & Liede (2002) transferred *N. columnaris* to a new genus, *Richtersveldia*, although both the statistical and morphological support for this change is very weak.

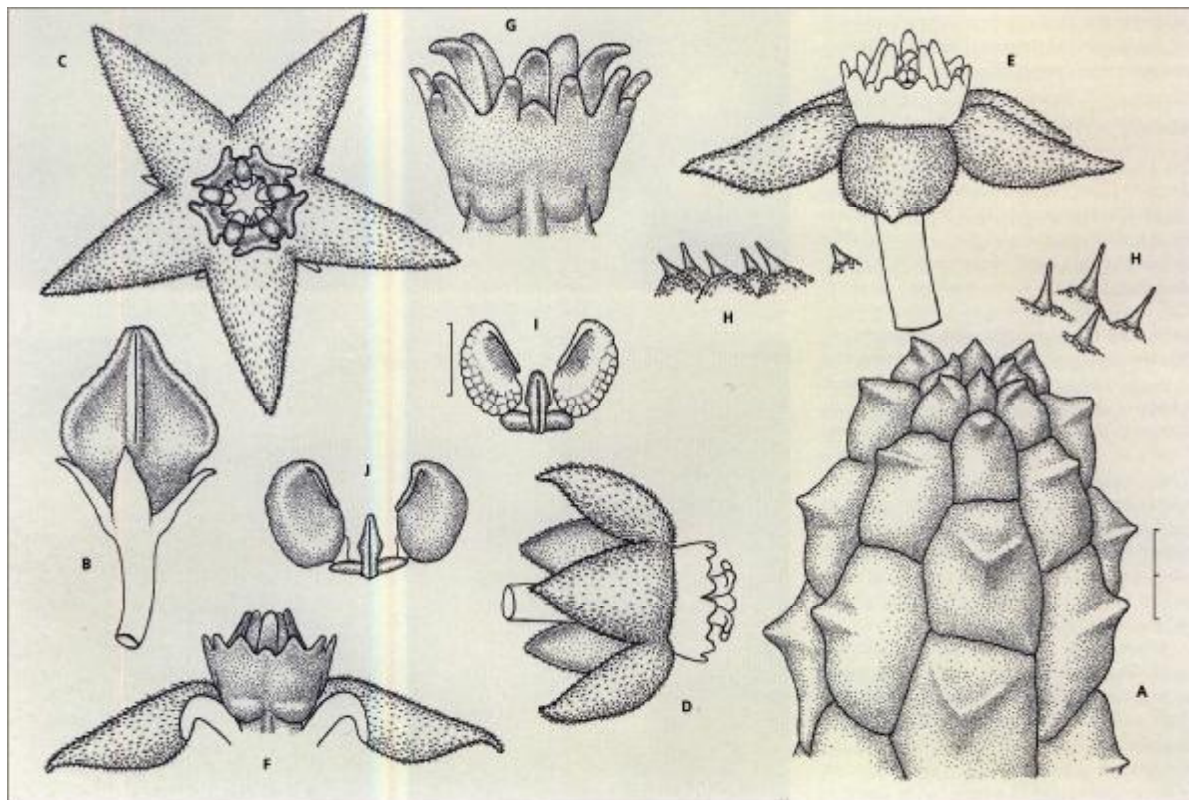


Fig. 8.1. *Notechidnopsis tessellata*. A, apex of stem. B, bud. C, face view of flower. D, E, side view of flower. F, side view of dissected flower. G, side view of gynoecium. H, papillae inside corolla: to left from near base of lobes; to right from around mouth of tube. I, J, pollinarium. Scale bars: A, B, C, D, E, F, 2 mm (at A); G, 1 mm (at A); H, I, J, 0.25 mm (at I). Drawn from: A, PVB 1092, foot of Vanrhyn's Pass; B, C, G, I, Van Breda 496; D, PVB 1101, Grasberg, Nieuwoudville; E, F, PVB 1088, foot of Vanrhyn's Pass; J, Kurzweil, near Loeriesfontein.

Notechidnopsis tessellata

Notechidnopsis tessellata (Pillans) Lavranos & Bleck, *Cact. Succ. J. (US)* 57: 256 (1985).

Caralluma tessellata Pillans, *Bull. Misc. Inform.* 1933: 187 (1933).

Type: South Africa, near road between South River and Nuwerus, Oct. 1929, Ross Frames sub NBG 198/31 (BOL, holo.; K, iso.) 2

Caralluma serpentina Nel, *Jahrb. Deutsch. Kakt.-Ges.* 3: 23 (1935).

Echidnopsis serpentina (Nel) A.C. White & B. Sloane, *Stap.*, ed. 2, 3: 987 (1937).

Type: Cape, Vanrhynsdorp, June 1931, Herre sub SUG 6945 (BOL, holo.; K, iso.).

Echidnopsis framesii A.C. White & B. Sloane, *Stap.*, ed. 2, 3: 985 (1937).

Type: as for *N. tessellata*.

Small succulent forming eventually a tangled mat up to 300 mm diam. Stems 30-150 mm long, 9-15 mm thick, prostrate to decumbent, sometimes slightly rhizomatous, green to purplish green; *tubercles* 1-2 mm long, 4-6-sided, flattish rising to obtuse tooth in middle, arranged into 6-8 very low obtuse rows along stems. *Inflorescences* 1-10 mainly in upper half of stem especially on new growth, each with 1-3 (-5) flowers; *pedicel* 3-5 mm long, < 1 mm thick, ascending to spreading and holding flower facing horizontally or upwards; *sepals* $\pm$ 1.5 mm long, < 1 mm broad at base, ovate-lanceolate, pale green. *Corolla* 6-10 mm diam., $\pm$ rotate; outside greyish white, glabrous; inside red-brown to red-purple usually speckled with pale yellow, becoming uniformly pale yellow towards centre, covered with sharp-pointed bristles (up to $\pm$ 0.15 mm long) each arising from a conical-obtuse papilla; *tube* shallow, cupular, containing at most lower third of gynostegium; *lobes* 2-4 mm long, 1.5-3.0 mm broad at base, spreading to reflexed, ovate-deltate, acute, margins folded so that inside strongly convex. *Corona* 2.0-2.5 mm tall, $\pm$ 3.0 mm broad, consisting of 2 series of lobes arising on staminal tube and partly intergrown, bright sulphur-yellow, glabrous; *outer lobes* $\pm$ 1.5 mm long, steeply ascending and sometimes spreading towards apices, bifid into obtuse linear recurved lobules to emarginate-truncate, fused laterally for lower two thirds with dorsal projections of inner lobes into deep cup hiding guide-rails; *inner lobes* 0.6-1.1 mm long, adpressed to backs of anthers at bases then erect as anthers become horizontal and sometimes recurved towards tips, dorsiventrally flattened, linear, obtuse, with

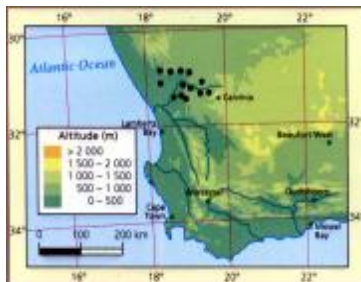


Fig. 8.5. Distribution of *Notechidnopsis tessellata*.

small truncate-erect dorsal projection in series with and laterally fused to outer lobes. *Anthers* horizontal on top of style-head, margins shrinking back to expose pollinia, rectangular. *Pollinium* ellipsoidal, longer than broad, insertion-crest exactly along outer edge, caudicle attached with small $\pm$ circular pad to ventral surface. *Follicles* erect, terete-fusiform, obclavate, slender, consisting of 2 horns diverging at 30-60°, longitudinally mottled with narrow broken purple stripes, glabrous, smooth.

Distribution and habitat

Notechidnopsis tessellata is endemic to the southern edge of Namaqualand, where it occurs from Vanrhynsdorp to Nuwerus and Bitterfontein and eastwards towards Loeriesfontein. Here it is found mainly in the hills and mountains around the basin of the Sout, Doring and Hantam rivers, at altitudes of 300-700 m. Specimens are almost always found on the lower slopes of dry hills, usually on shales and never on the quartz patches which are well-known and characteristic of the Knersvlakte. Plants tend to seek protection among and under stones and under small bushes and are rarely found even partially exposed. In some localities this is quite a common plant but it is inconspicuous and easily overlooked.

Diagnostic features and relationships

Plants of *N. tessellata* have prostrate to decumbent stems which form sometimes quite extensive and dense mats. There is little of the rhizomatous tendency of *Richtersveldia columnaris* to be found here, although occasional stems spread underground (often under stones) for short distances.

The stems are slender and cylindrical with low and obscure tubercles (fig. 17 F) and this gives them a tessellate, almost snake-like appearance.

Like most stapeliads that produce plenty of stems, the primary stem here does not bear flowers, which are instead borne on the side-branches. They appear in large numbers mainly towards the tips of new growth, although older inflorescences may be re-activated to produce flowers so that they can be found occasionally lower down on stems too. In *N. tessellata* all the bracts in the inflorescence are flattened and they have a quite different shape to the tubercles.

The outside of the flower is a characteristic pale, usually cream colour. Inside, while quite variable, they are usually reddish brown to reddish purple finely flecked with pale yellow. This pattern changes to plain pale yellow towards the centre around and inside the tiny tube. The flowers emit a strong, sourish, honey-like scent which is detectable up to 20 cm away from a single flower. They are small (not exceeding 10 mm across), with a very small tube in the centre which only contains the base



Fig. 8.2. *N. tessellata*, PVB 4581, north-east of Bitterfontein.



Fig. 8.3. *N. tessellata*, R. Nagel, Brandkop, north of Nieuwoudville.



Fig. 8.4. *N. tessellata*, PVB 6020, north of Vanrhyn's Pass.

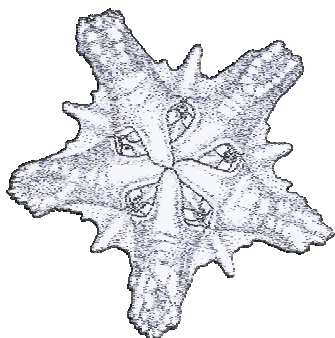
of the gynostegium. The lobes are spreading to reflexed and in the latter case they push the corona somewhat forward.

The corona is bright yellow and consists of a cup-like outer series surrounding the whole structure and small, flattened inner lobes which are initially pressed to the backs of the anthers but then rise up and spread above them.

History

Notechidnopsis tessellata was discovered by Percy Ross Frames in October 1929 on the northern Knersvlakte somewhere between the Sout River and Nuwerus. It has sometimes been regarded as very rare (Hall 1957) but this is not an accurate view of the situation as many collections have been made over the years and it is of fairly general occurrence around and on the Knersvlakte.

9. Ophonella



The genus *Ophonella* was described in 1981 to accommodate the species *Pectinaria arcuata* and *P. mirkinii* which did not fit into either *Pectinaria sensu stricto* or *Stapeliopsis*, where some of the other species of *Pectinaria* in the broad sense of N.E. Brown were moved (Bruyns 1981a). Since then, a further species has been discovered in the mountains around Willowmore in the Eastern Cape province of South Africa and this was described recently as *Ophonella willowmorensis* (Bruyns 1999e).

Meve & Liede (2002) included only one species of *Ophonella* and their data did not resolve its relationships. Our own molecular investigations of *Stapeliopsis* (Bruyns *et al.* 2005) included both species of *Ophonella* and showed that *Ophonella* formed a strongly supported monophyletic entity which, when both molecular and morphological data were included, is sister to *Stapeliopsis* and the group of stapeliads (including *Orbea* and *Huernia*) in which basal inflorescences with few and often fairly large flowers predominate.

Ophonella Bruyns, *Cact. Succ. J. Gr. Brit.* 43: 70 (1981).

Type: *Ophonella arcuata* (N.E. Br.) Bruyns.

Dwarf spineless non-rhizomatous succulent forming prostrate mat 60-150 mm diam. Stems 20-250 mm long, 3-8 mm thick, prostrate with tips ending under soil surface, glabrous, brownish green to nearly black; tubercles < 1 mm long, conical but low and scarcely rising out of stem, not laterally flattened, arranged into 4 rows along stem so stem square in cross-section, abruptly narrowing into minute ridge-like tooth just beneath next tubercle, without stipular denticles. Inflorescences 1 (-4) per stem arising near base, each with 1-4 flowers developing in gradual succession on short peduncle (up to 10 mm long but not more than 1.5 mm thick) with a few slender lanceolate-acuminate bracts up to 1.5 mm long sometimes with lateral teeth; pedicel 1-4 mm long, 0.5-1.0 mm thick, spreading then ascending to hold flower facing upwards; sepals 0.8-2.0 mm long, ovate-lanceolate, acuminate. Corolla 3.5-4.0 mm long, 4-12 mm diam., from ± spherical to acuminate and bud-like or campanulate, shallowly lobed; outside glabrous, smooth to papillate, pink to white; inside

smooth to papillate and sometimes with erect rigid hairs, white or cream with deep red patches; tube 1.75-4.00 mm long, 3-7 mm broad at mouth, ovoid to hemispherical or shallowly bowl-shaped; lobes 3-9 mm long, 2-5 mm broad at base, ascending and joined at tips over centre of flower to spreading, deltate to narrowly deltate, acute to acuminate, margins ciliate. Corona 0.5-1.5 mm tall, 1.5-4.0 mm broad, consisting of 2 series of lobes arising on staminal tube and partly intergrown, raised on a very short stipe up to 0.5 mm long, bright yellow to cream; outer lobes up to 0.5 mm long, spreading and slightly ascending, consisting of small central obtuse ventrally keeled tooth beneath guide-rails spreading laterally to prominent ascending to spreading swollen to flattened projection behind anthers up to 1 mm long often with tubercled upper surface or toothed margin; inner lobes < 0.7 mm long, adpressed to backs of anthers and often exceeding them slightly to meet in centre, dorsiventrally flattened, deltoid and obtuse to subquadrate-emarginate. Anthers horizontal on top of style-head, margins shrinking back to expose pollinia, rectangular. Pollinium ellipsoidal, broader than long, insertion-crest exactly along outer edge, caudicle attached with small ± circular pad to ventral surface. Follicles erect, terete-fusiform, obclavate, slender but short (< 35 mm long), consisting of 2 horns diverging at 30-60°, longitudinally mottled with narrow broken purple stripes, glabrous, smooth.

Although the plants of *Ophonella* are generally hard to find, they are not always that small and may form clumps up to 300 mm in diameter. Such clumps consist of large numbers of interwoven and entangled 4-angled stems which are more or less square in cross-section. At 3-6 mm thick these stems are among the more slender to be found among the stapeliads. They are prostrate, usually adpressed to the surface of the soil or partly submerged in it (with just the upper surface above the ground) and they produce roots along their entire length on the undersurface. The stem may continue growth for up to 100 mm or more but eventually the terminal bud ceases growth (usually when in a slightly submerged position) and growth then continues from axillary buds towards the base. Spaced out along the stems are rectangular but only slightly raised tubercles, each of which bears a small and inconspicuous tooth just beneath the beginning of the next tubercle.

Flowers are borne on a few small inflorescences near the base of the stem. Each inflorescence develops a tiny peduncle with minute concave bracts on it. The small corolla is usually not much more than 6-8 mm long or broad (reaching a maximum of 14 mm long) and

is usually cream or white with deep red inside. It has a bowl-shaped to cupular tube which is often thickened around the mouth and is quite a bit taller than the gynostegium. At the mouth of the tube there are small deltate lobes which may remain fused at their tips (in which case the flower has a bud-like shape) or may spread out fully, in which case it is somewhat bell-shaped.

In both species the bright yellow corona is seated on a short stipe at the bottom of the tube and is much broader than tall. The outer series consists of small, narrow lobes beneath the guide-rails which are keeled on their upper surface and are joined laterally to much broader, usually somewhat irregularly toothed structures behind the anthers. So the outer series, in fact, spreads right around the gynostegium. The small, flattened inner lobes are adpressed to the backs of the anthers.

The two species of *Ophonella* are found only in the dry parts of the Eastern Cape of South Africa, in a small region from Willowmore eastwards to near Grahamstown and from Pearston southwards to near Port Elizabeth. It is the only stapeliad genus that is endemic to the Eastern Cape.

As far as is known, the two species inhabit quite different ecological niches. *Ophonella arcuata* is mainly found in low-lying, flat areas in valleys and is often associated with a small, gregarious species of *Drosanthemum* or a spiny *Ruschia*. It also inhabits low, gravelly slopes under small karroid bushes. On the other hand, *O. willowmorensis* occurs on steep, north-facing, sandstone slopes under small bushes on rock slabs and rock outcrops in succulent enclaves (usually associated with *Euphorbia polygona*), that are surrounded by arid fynbos.

In the field, plants are extremely difficult to locate owing to the manner in which the narrow, brownish green, snake-like stems become covered with leaf-litter, mud and other debris under the small shrubs beneath which they always grow (fig.9.4). This has led to their being remarkably little known. In fact, the only local inhabitant that I have ever met who knew *O. arcuata*, a Mrs. Kleynhans of Willowmore, had found it inadvertently when trying to locate the nest of a small bird: when lifting up the bush from which the bird had shot out in surprise, she noticed this peculiar plant and later brought it to the attention of M. Bruce Bayer, who was then curator of the Karoo Botanic Garden.

Key to the species

Outside of corolla papillate, inside banded with deep red on white, with hairs

up to 1 mm long

2. *O. willowmorensis*

Outside of corolla smooth, inside maroon in base, rest cream, without hairs

1. *O. arcuata*

1. *Ophionella arcuata*

Ophionella arcuata (N.E.Br.) Bruyns, Cact. Succ.
J. Gr. Brit. 43: 72 (1981).

Pectinaria arcuata N.E. Br., Fl. Cap. 4 (1): 870 (1909).
Type: South Africa, Eastern Cape, 9 miles south-south-
east of Bedford, July 1903, N.S. Pillans 182
(K, holo.; BOL, iso.).

Stems 40-250 mm long, 3-8 mm thick. *Pedice!* 1-4 mm long, 0.75-1.00 mm thick. *Corolla* 5-14 mm long, 6-12 mm diam., bud-like to campanulate; outside glabrous and smooth, cream often suffused with pink; inside smooth, cream on lobes and mouth of tube changing abruptly to maroon lower in tube (sometimes with narrow cream patch around base of corona); *tube* 3-6 mm long, 2-7 mm broad at mouth, narrowly to broadly cupular, with corolla somewhat thickened at mouth; *lobes* 3.5-9.0 mm long, 2.0-4.8 mm broad at base, ascending and joined at tips to spreading, narrowly deltate to deltate, acuminate to acute, slightly convex inside. *Corona* 10-15 mm tall, 2-4 mm broad, raised on very short obtusely pentagonal stipe < 0.5 mm long, bright yellow to cream, occasionally

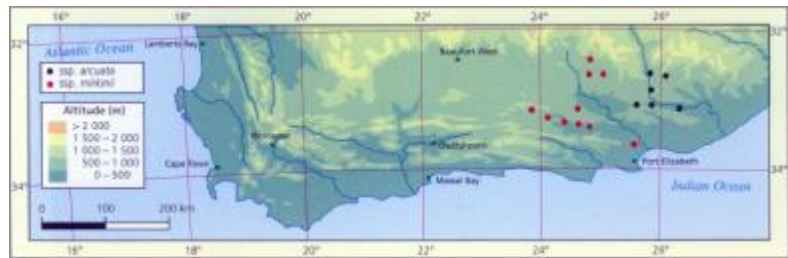


Fig. 9.1. Distribution of *Ophionella arcuata*.

with maroon patches on sides of dorsal projection of inner lobes; *outer lobes* spreading, $\pm$ truncate with obtuse central thickened tooth, joined laterally to prominent swollen truncate ascending to spreading projection behind anthers up to 1 mm long slightly exceeding height of style-head and often with tuberculate upper surface, < 0.5 mm long; *inner lobes* 0.50-0.75 mm long, adpressed to backs of anthers and sometimes exceeding them to touch in centre, dorsiventrally flattened.

Although *O. arcuata* was discovered as early as 1903, it remains known from only a few collections. In comparison to *O. willowmorensis* it is quite widespread, as it has been collected in the area between Willowmore, Port Elizabeth and the Dikop Flats, which lie to the north of Grahamstown. This gives it a range of roughly 250km. It is actually a relatively common plant where it occurs and, in some localities, upwards

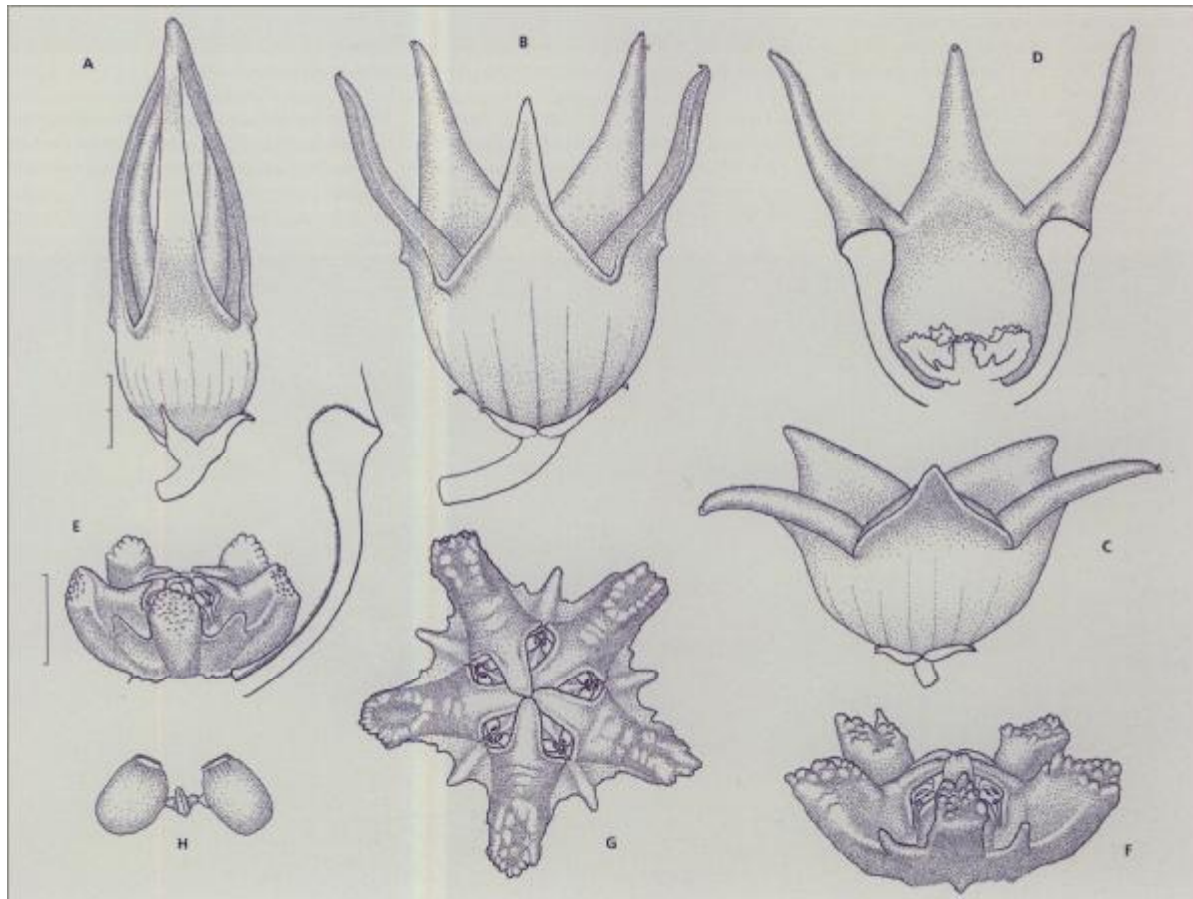


Fig. 9.2. *Ophionella arcuata* (A, E, subsp. *arcuata*; rest subsp. *mirkinii*). A-C, side view of flower. D, side view of dissected flower. E, F, side view of gynostegium. G, face view of gynostegium. H, pollinarium. Scale bars: A-D, 2 mm (at A); E-G, 1 mm (at E); H, 0.25 mm (at A). Drawn from A, E, PVB 5010, Dikop flats, north of Grahamstown; rest PVB 4257, near Baroe Siding.

OPHIONELLA ARCUATA

of 15 specimens have been seen, though these are usually only revealed by careful and diligent searching.

Ophionella arcuata has small flowers (rarely more than 8-10 mm across) which face upwards among the stems. The outside of the flower is an unexciting cream suffused with pink. Inside, however, they are quite dramatically coloured, with cream on the lobes and around the mouth of the tube which changes abruptly to dark maroon lower in the tube.

The colour of the corolla contrasts again with that of the striking, yellow corona. In *O. arcuata*, behind each inner lobe there is a broad, relatively massive appendage and these structures dominate the gynostegium. They are spreading to somewhat ascending and usually have a tuberculate upper surface. The small outer lobes fill in the gaps between them beneath the guide-rails.

Ophionella arcuata is very variable in the length and breadth of the corolla tube and lobes. Plants with relatively long and slender lobes mostly occur towards the eastern side of the range of the species and, in these, the lobes invariably remain joined at their tips. Towards the western side the lobes are a lot shorter and broader and in such flowers they usually (but not always) become free at their tips and may spread out widely, then revealing fully the pretty colouring of the inside of the flower. There is also a gradual transition, as one moves westwards, from a more or less ovoid tube to

Key to the subspecies of <i>O. arcuata</i>	
Corolla lobes remaining joined at tips at anthesis, more than twice as long as broad at base, corolla tube 2.5-5.0 mm diam.	1a. subsp. <i>arcuata</i>
Corolla lobes free at anthesis, erect to spreading, less than twice as long as broad at base, corolla tube 5-7 mm diam.	1b. subsp. <i>mirkinii</i>



Fig. 9.3. *O. arcuata* subsp. *arcuata*, PVB 5010, Dikkop Flats, north of Grahamstown.

a broader, cupular tube and together with this trend, the corona also becomes broader. As a consequence of these transitions, the two species *Pectinaria arcuata* and *P. mirkinii* are not clearly separable into discrete taxa.

Nevertheless, the partial separation that exists is clearly geographical and so these two are recognised at the rank of subspecies (Bruyns 1999e).



Fig. 9.4. *O. arcuata* subsp. *arcuata*, PVB 1572, near Middleton, plant in habitat, with the stems partly buried in leaf-litter under a plant of *Ruschia spinosa*, December 1977.

1a. *Ophionella arcuata* subsp.
arcuata

Corolla bud-like; tube up to 4 mm long and 2.5-5.0 mm broad, narrowly cupular; lobes 6-9 mm long, 2-3 mm broad at base, remaining attached at tips, narrowly deltate, acuminate. Corona 1.0-1.5 mm tall, 2.0- 2.3 mm broad, bright yellow.

Distribution and habitat

Subsp. *arcuata* is mainly associated with the valley of the Great Fish River between Cookhouse in the north and Anne's Villa and Kom-madagga (on the northern foot of the Suurberg) eastwards to the Dikkop Flats, north-west of Grahamstown. The type was collected slightly east of Cookhouse near Bedford. This subspecies therefore occupies the eastern part of the distribution of the species.

Diagnostic features and relationships

Subsp. *arcuata* can be recognised by the comparatively long, narrowly deltate corolla lobes which are usually fused at their tips, as well as the narrower tube and the somewhat narrower gynostegium. Examination of the surface of the inside of the corolla with the SEM has shown that the outer walls of the epidermal cells are usually round-tipped and very short. Flowers have been observed (PVB 501) with a distinct cream area inside the tube towards the base below the maroon patch but this is not constant. The corona has always been found to be bright yellow.

History

This subspecies was discovered by N.S. Pillans near Bedford in 1903.



Fig. 9.5. *O. arcuata* subsp. *mirkinii*, PVB 4257, near Baroe Siding, flowers with somewhat darkened tips to the lobes.

1b. *Ophionella arcuata* subsp.
mirkinii

Ophionella arcuata subsp. *mirkinii* (Pillans)

Bruyns, J. Linn. Soc. Bot. 131: 395 (1999).

Pectinaria mirkinii Pillans, J. S. African Bot. 5: 64 (1939).

O. arcuata var. *mirkinii* (Pillans) Bruyns, Cact. Succ. J. Gr. Brit. 43: 73 (1981).

O. mirkinii (Pillans) Plowes, Excelsa 20:19 (2003).

Type: South Africa, Eastern Cape, Steytlerville, Mirkin sub BOL 22432 (BOL).

Corolla campanulate; tube 2.5-5.0 mm long, 5-7 mm broad, broadly cupular; lobes 4-5 mm long, 3-5 mm broad at base, erect to spreading (free at apices), deltate, acute. Corona 1.00-1.25 mm tall, 2.8-4.0 mm broad, cream to bright yellow.

Distribution and habitat

Subsp. *mirkinii* occupies the western part of the distribution range of the species from Knoetze siding, a little east of Willowmore, through Steytlerville (where several collections have been made around Springbokvlakte) to near Port Elizabeth. It is also found around Pearson to the west of Somerset East.

Diagnostic features and relationships

Vegetatively the two subspecies are indistinguishable.

Florally subsp. *mirkinii* is usually easily identified by the broader, erect to spreading corolla lobes and the broader corolla tube. In material from around Springbokvlakte the epidermal cells inside the corolla (especially



Fig. 9.6. *O. arcuata* subsp. *mirkinii*, PVB 4917, east of Steytlerville. One flower has been cut open to show the colouring of the corolla tube inside.

towards the base) are longer and narrower than those seen in subsp. *arcuata*. Flowers of subsp. *mirkinii* seem to lack the cream patch in the base of the tube around the corona and are maroon right to the base of the gynostegium. In one collection (PVB 4257) the corolla lobes were tipped with red as well. The corona is cream in material from Willowmore to near Port Elizabeth but, in that from near Pearson, it is bright yellow.

History

Subsp. *mirkinii* was first collected by Ronald James (1917-?), the son of H.W. James (see under *Huernia kennedyana*), near Port Elizabeth in May 1938. The material from which it was described was discovered near Steytlerville by Eliezer David 'Lazar' Mirkin (?1883-23 August 1940), a Lithuanian Jewish wholesaler who lived in Port Elizabeth and was a keen naturalist. His collection was drawn at the Bolus Herbarium in February 1939 and it was described in the same year.



Fig. 9.7. *O. arcuata* subsp. *mirkinii*, PVB 4257, near Baroe Siding.

OPHIONELLA WILLOWMORENSIS

2. *Ophionella willowmorensis*

Ophionella willowmorensis Bruyns, J. Linn. Soc. Bot. 131:396(1999).

Type: South Africa, north-east of Willowmore, Bruyns 4966 (BOL, holo.; K, iso.).

Stems 30-150 mm long, 3-5 mm thick, often somewhat subterranean, then slender and becoming thicker on emerging. Pedicel 1.5-6.0 mm long, 0.50-0.75 mm thick, glabrous, ascending; sepals ± 1 mm long, 0.25-0.50 mm broad at base, transparent-white, ovate-acuminate, papillate. Corolla 3.5-7.0 mm long, 4-6 mm broad (usually broadest just beyond mouth of tube), bud-like and broadly elliptical to nearly spherical to depressed-globose; outside white to white at base speckled with pale red above coalescing on lobes, glabrous, with small obtuse conical papillae except towards base; inside smooth, with bold irregular deep red spots on lobes and 3 concentric deep red rings in tube all on white background, with stiff erect cylindrical white to red hairs up to 1 mm long in tube and to $\pm$ middle of lobes; tube 1.5-2.0 mm long, 3.0-4.5 mm broad, shallowly bowl-shaped, not thickened at mouth; lobes 3-5 mm long, 2.0-3.3 mm broad at base, ascending then becoming horizontal or descending towards apices where remaining fused, deltate, acuminate, slightly convex inside. Corona ± 12 mm tall, 1.5-2.5 mm broad, raised on short cylindrical stipe ± 0.5 mm long, bright yellow, sometimes flecked with red on backs of inner lobes; outer lobes ± 0.5 mm long (usually exceeding dorsal projection of inner lobe), ascending, lanceolate-obtuse to acuminate, joined laterally to horizontally spreading flattened projection apically divided into 4-5 obtuse teeth; inner lobes ± 0.25 mm long, deltoid to subquadrate, emarginate, adpressed to backs of anthers and usually shorter than them, dorsiventrally flattened.

Distribution and habitat

Ophionella willowmorensis is endemic to the mountains north-east of Willowmore. It was first gathered in crevices on sandstone slabs at about 1 200 m in the Witteberg. More recently it has been located approximately 10 km south-west of this, also in the Witteberg, and a further 20 km to the west on the rocky, northern aspect of the Boesmanspoortberge.

All these places are most unexpected in view of the predictability of the habitat of *O. arcuata*. In contrast to the flat, low-lying habitats of *O. arcuata*, those occupied by *O. willowmorensis* are steep, north-facing sandstone slopes. Generally plants grow under small bushes in crevices on rock slabs, in small tufts of grass or clumps of the small composite shrub *Dolichotheix ericoides* or in rocky places with shallow soils. Generally these are spots with a profusion of other succulents, though they are surrounded at higher levels by arid *fynbos*. In several localities the species has been found in association with *Euphorbia polygona*. Plants grow hidden in small accumulations of leaf-litter with only occasional pieces of stem arching out of this cover and becoming exposed.

Diagnostic features and relationships

In *O. willowmorensis* some of the stems spread as thin runners for up to 80 mm or more beneath the soil and under stones, becoming thicker once more on emerging. Exposed pieces of stem become very dark and may often be nearly black. The stems are generally a darker, brownish green and have more obscure tubercles than those of *O. arcuata* but

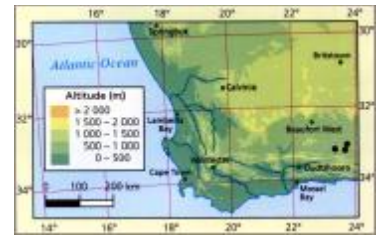


Fig. 9.8. Distribution of *Ophionella willowmorensis*.

otherwise the stems of the two species are not easily separated.

Florally, however, they are significantly different. The flowers are, as usual, produced on small inflorescences arising near the bases of the stems. There may be up to four small clusters of flowers around the base of one stem, particularly on the younger, shorter stems. Many of these younger stems branch from an older stem and grow initially slightly beneath the surface of the soil. In such cases the flowers arise on small, slender, knobby white subterranean peduncles which may be up to 10 mm long. On the other hand, peduncles above the soil are rarely more than 1 mm long. Similarly those pedicels that arise beneath the soil may be up to 6 mm long, so as to bring the flower to the surface, while those developing above the surface are often only 1.5 mm long. Flowers arising under the soil develop more or less at the surface with the cage formed by the lobes projecting from the ground and the rest remaining beneath it. Such flowers often become partly filled with sand and small pieces of leaf-litter.

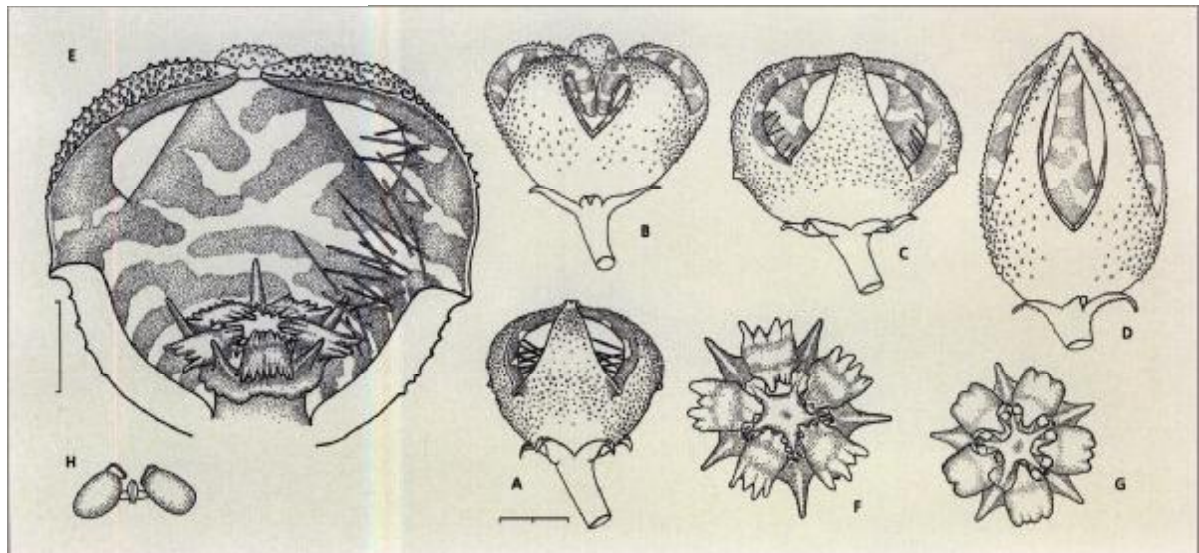


Fig. 9.9. *Ophionella willowmorensis*. A-D, side view of flower. E, side view of dissected flower. F, G, face view of gynostegium. H, pollinarium. Scale bars: A-D, 2 mm (at A); E-G, 1 mm (at E); H, 0.25 mm (at A). Drawn from A, D-F, H, PVB 4966, Witteberg; C, PVB 7098, Witteberg; B, G, PVB 6317, Boesmanspoortberge.

The flowers are small and shortly elliptical to nearly spherical, with the lobes remaining joined at their tips and often somewhat depressed into the flower. The pale white to reddish exterior has many small papillae on it, each of which is, in fact, a much elevated stoma (as in fig. 25 C, D). The inside is boldly marked with irregular deep red bars on the lobes and three concentric rings of deep red inside the tube, all on a white background. There are white to red hairs on the inside which project straight out from the surface towards the centre. The background cells have sharply pointed outer walls (fig. 26 D).

The outer corona is also significantly different. It has quite long, relatively slender lobes beneath the guide-rails and thin, horizontally spreading projections behind the inner lobes, rather than the massive, solid boss behind each of them that characterises the corona of *O. arcuata*.

History

Ophionella willowmorensis was discovered in January 1992 during exploration of the Witteberg, to the north-east of Willowmore. I have been unable to trace any previous records of this species and it is one of the few new stapeliads to appear in southern Africa in recent years.

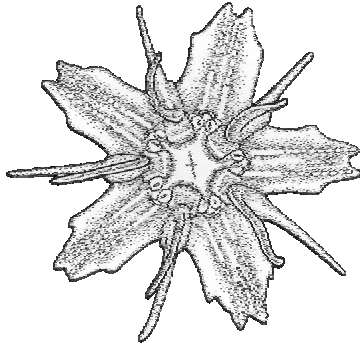


Fig. 9.10. *O. willowmorensis*, PVB 6317, Boesmanspoortberge.



Fig. 9.11. *O. willowmorensis*, PVB 4966, Witteberge. The papillate exterior of the corolla is clearly visible here as are the bright markings inside.

10. Orbea



Orbea was created by Haworth for a miscellany of species. It was typified by Pfeiffer (1872) by *O. maculosa* which is a hybrid that had appeared in cultivation in Europe and is not known in the wild. In 1975 Leach resurrected the genus *Orbea* but selected *O. variegata* as lectotype (Leach 1975). He made several errors here. One was that he was unaware of

Pfeiffer's earlier valid lectotypification of *Orbea* (Mottram 1996). As a consequence, by choosing a new lectotype, he created a new genus *Orbea* L.C. Leach which, of course, was illegitimate since the name *Orbea* already existed. The second error that he made was that he seems to have convinced himself that Linnaeus, who in 1753 knew only *Stapelia hirsuta* and *S. variegata*, considered *S. hirsuta* more to represent his concept of *Stapelia* than *S. variegata*. As pointed out by Hunt (1979), there is evidence in Linnaeus' own writing that would make *S. variegata* the undisputed type of *Stapelia* and it remains a mystery what convinced Leach that the opposite was true (though see Leach 1981). This issue was partly resolved by the conservation of *Stapelia* with *S. hirsuta* as the type (Brummitt 1995). Final resolution was achieved with the conservation of *Orbea* with *O. variegata* as the type (Bruyns 1998c; Brummitt 2000).

So, finally, after lengthy 'legal' proceedings, *Orbea* Haw. is typified by *O. variegata* and *Stapelia* by *S. hirsuta*. When he reviewed *Orbea* in 1978, Leach

erected three new genera for several groups of species which are closely related to those that he placed in *Orbea*: *Orbeopsis* for the '*Caralluma lutea*' group; *Pachycymbium* for *Caralluma carnosa* and *C. keithii*, and *Orbeanthus* for *Stultitia conjuncta* and *S. hardyi*. More recently, the genus *Pachycymbium* was modified by Gilbert (1990) to include four other species from southern Africa (*lugardii*, *C. rogersii*, *C. ubomboensis* and *Stultitia miscella*) and a group of species from tropical Africa and Arabia which mainly occur north of the equator, particularly in north-east Africa (with species in Arabia and one in West Africa) and which had formerly been known as the 'ango-group' of *Caralluma*. Plowes (1994b) moved the same four southern African species and the members of the 'ango-group' out of *Pachycymbium* into the genus *Angolluma* which had been established by R. Munster in 1990. It has been shown, however, that there is neither phylogenetic nor morphological support for all these genera. In particular, the vegetative variation that Leach was recognising with his various segregates

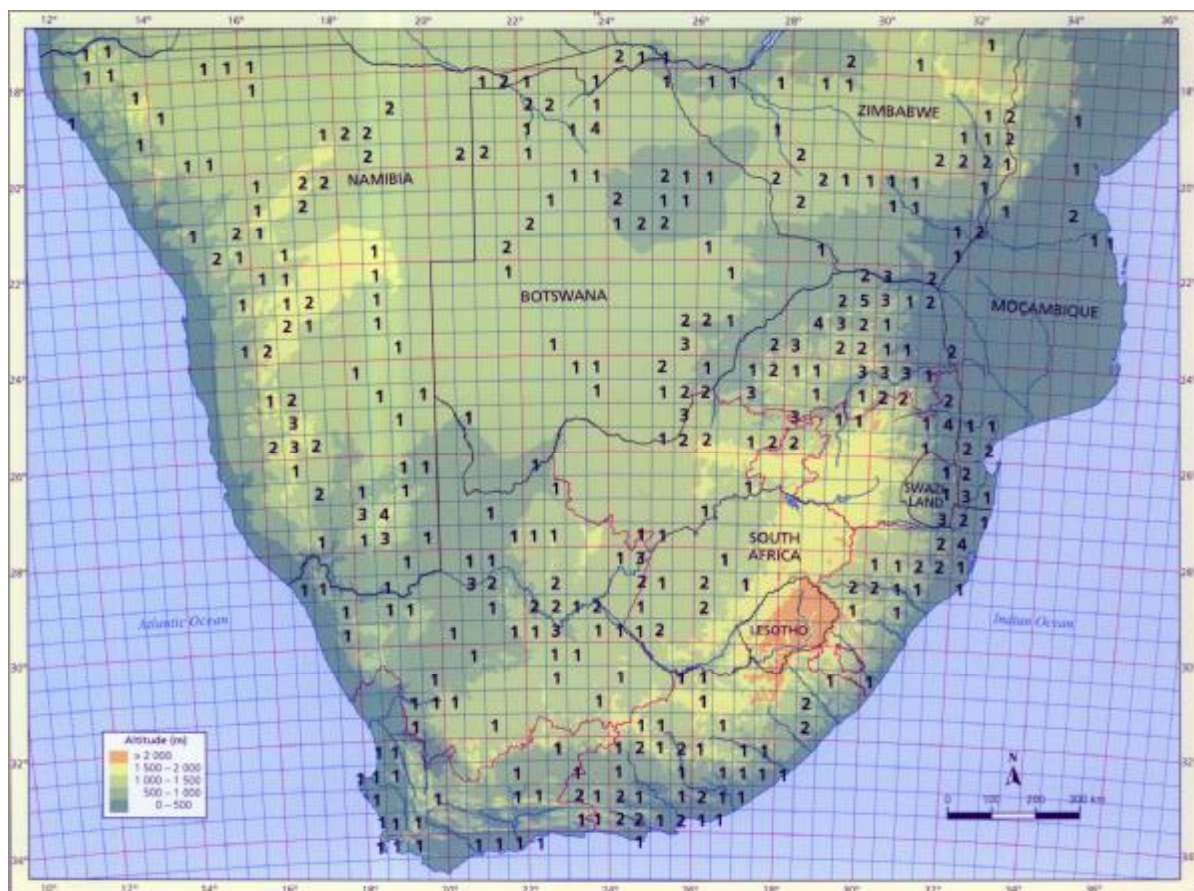


Fig. 10.1. Patterns of diversity in *Orbea* in southern Africa, showing the number of species recorded to date in each half-degree square.

from *Orbea* is to be seen in other genera such as *Duvalia*, *Hoodia*, *Huernia* and *Stapelia*. As a consequence of a detailed study and phylogenetic analysis, all of the genera were placed in an expanded *Orbea* (Bruyns 2001; 2002). Recent molecular investigations (Meve & Liede 2002) did not resolve the relationships of *Orbea* to other genera. Meve & Liede (2002) found that *Tridentea virescens* was nested within their '*Orbea* clade' and concluded that further gene regions were required to resolve this clade. Our own molecular investigations have shown that their position for *T. virescens* was undoubtedly a consequence of misidentified material and that *T. virescens* belongs (with very strong statistical support) to *Tridentea*. In our own research we have sampled widely from the expanded concept of *Orbea* to include 22 species. We have especially involved those whose positions have been more than usually difficult to decide upon from morphological data (such as *O. lugardii*, *O. miscella*, *O. paradoxa*, *O. rogersii*, *O. schweinfurthii* and *O. ubomboensis*). This work has revealed a large *Orbea*-branch which includes most of the species that Leach placed in *Orbea* (except, of course, for *O. prognatha*; see under *Duvalia*), most of the species placed in *Pachycymbium* by Gilbert (and in *Angolluma* by Plowes), all the species of *Orbeanthus*, *Orbeopsis* and also *O. lugardii*, *O. paradoxa*, *O. rogersii* and *O. schweinfurthii*. We have found that *O. maculata*, *O. miscella* and *O. ubomboensis* do not fall within this large grouping. Sister to the large *Orbea* group is *Tavaresia* and sister to these is a well-supported branch containing *Australiuma peschii* and *O. ubomboensis*. The relationships of *O. maculata* and *O. miscella* remain unresolved. The large *Orbea*-branch has also been found to include *Tromotriche longii*. *Orbea* is therefore left largely as it was in Bruyns (2002), except that *O. ubomboensis* has been removed and placed within *Australiuma* and *T. longii* is transferred to *Orbea*.

Orbea Haw., *Syn. Pl. Succ.*: 37 (1812), *nom. cons.*
Stapelia [unranked] *Orbeae* Schult. in Roem. & Schult., *Syst. Veg.* 6: 36 (1820).
Stapelia sect. *Orbea* (Haw.) Decne. in DC, *Prodr.* 8: 658 (1844).
Orbea sect. *Orbea* subsect. *Exstantes* L.C.Leach, *Excelsa Taxon. Ser.* 1: 6 (1978), *nom. superfl.*
 Lectotype: *Orbea variegata* (L.) Haw.
Podanthes Haw., *Syn. Pl. Succ.* 32 (1812).
Stapelia [unranked] *Podanthes* Schult. in Roem. & Schult., *Syst. Veg.* 6: 28 (1820).
Stapelia sect. *Podanthes* (Haw.) Decne. in DC, *Prodr.* 8: 655 (1844).
 Lectotype: *Podanthes verrucosa* (Masson) Haw.
 [= *Orbea verrucosa* (Masson) L.C.Leach].
Diplocyatha N.E. Br., *J. Linn. Soc. Bot.* 17: 167 (1878).
 Type: *Diplocyatha ciliata* (Thunb.) N.E. Br.
 [= *Orbea ciliata* (Thunb.) L.C.Leach].

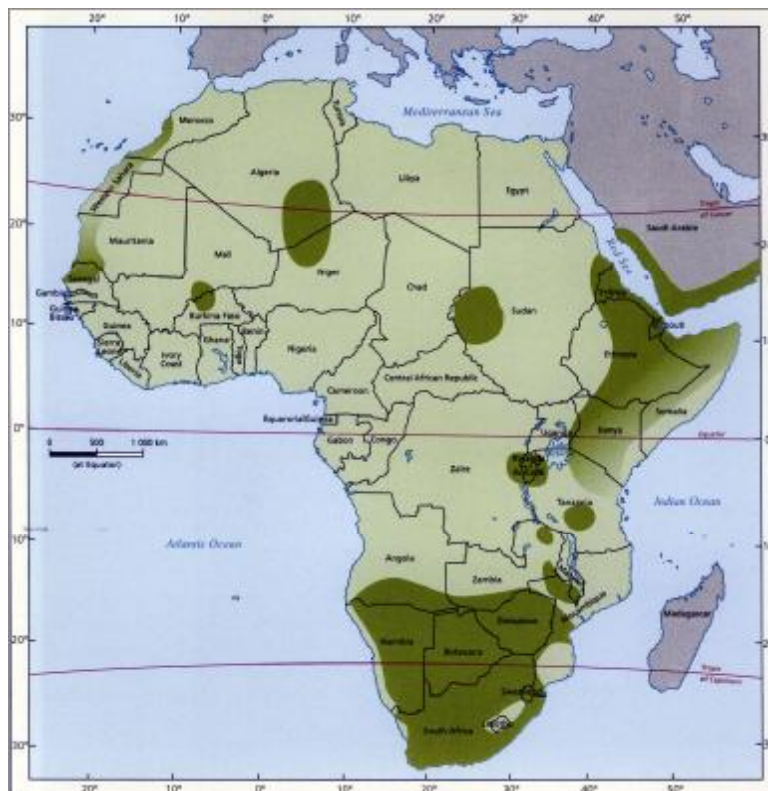


Fig. 10.2. Distribution of *Orbea*.

Stapeliopsis E.Phillips, *H. Pl. South Africa* 12: t. 445 (1932), *nom. illegit.*, non Pillans (1928) non Choux (1931).
Stultitia E.Phillips, *Fl. Pl. South Africa* 13: t. 520 (1933).
Orbea sect. *Stultitia* (E.Phillips) L.C.Leach, *Excelsa Taxon. Ser.* 1: 6 (1978).
Orbea sect. *Stultitia* subsect. *Confluentilobae* L.C.Leach, *Excelsa Taxon. Ser.* 1: 6 (1978).
 Type: *Stapeliopsis cooperi* (N.E. Br.) E.Phillips [= *Orbea cooperi* (N.E. Br.) L.C.Leach].
Orbea sect. *Orbea* subsect. *Inspissatae* L.C.Leach, *Excelsa Taxon. Ser.* 1: 6 (1978).
 Type: *Orbea verrucosa* (Masson) L.C.Leach.
Orbea sect. *Stultitia* subsect. *Carentilobae* L.C.Leach, *Excelsa Taxon. Ser.* 1: 6 (1978).
 Type: *Orbea maculata* (N.E. Br.) L.C.Leach.
Orbea sect. *Codonidium* L.C.Leach, *Excelsa Taxon. Ser.* 1: 6 (1978).
 Type: *Orbea paradoxa* (L.Verd.) L.C.Leach.
Orbeanthus L.C.Leach, *Excelsa Taxon. Ser.* 1: 71 (1978).
 Type: *Orbeanthus conjunctus* (A.C.White & B.Sloane) L.C.Leach [= *Orbea conjuncta* (A.C.White & B.Sloane) Bruyns].

Orbeopsis L.C.Leach, *Excelsa Taxon. Ser.* 1: 61 (1978).
 Type: *Orbeopsis lutea* (N.E. Br.) L.C.Leach [= *Orbea lutea* (N.E. Br.) Bruyns].
Pachycymbium L.C.Leach, *Excelsa Taxon. Ser.* 1: 69 (1978).
 Type: *Pachycymbium keithii* (R.A.Dyer) L.C.Leach [= *Orbea carnosa* subsp. *keithii* (R.A.Dyer) Bruyns].
Angolluma Munster, *Cact. Succ. J. (Woollahra)* 17: 63 (1990).
 Type: *Angolluma decaisneana* (Lem.) L.E.Newton [= *Orbea decaisneana* (Lem.) Bruyns].

Spineless often rhizomatous succulent forming compact to diffuse clumps (occasionally very large, up to 3 m diam.). Stems decumbent to prostrate, fleshy and firm, glabrous, 10-300 mm long, 4-25 mm thick (excluding teeth), mottled with purple-brown on green to grey-green (rarely plain brownish); *tubercles* (1-) 4-25 mm long, deltoid to conical, spreading, often laterally flattened and joined into 4 wings along stem (sometimes only loosely arranged into 4 rows along stem), each tipped with soft acute to acuminate leaf-rudiment (rarely hardened at tip) usually subtended by 2 stipular denticles. *Inflorescences* glabrous, 1-3 (-5) per stem, arising at any height on stem, each bearing 1-40 flowers developing in gradual to rapid succession (or opening simultaneously) from

Key to the species

1. Inflorescence with (3-) 4-40 flowers opening in quick succession to $\pm$ simultaneously 2.
2. Inner corona lobes not much produced beyond anthers and not rising in centre (always dorsiventrally flattened), without any dorsal outgrowths 5. *O. caudata*
2. Inner corona lobes much produced beyond anthers to become erect and often recurved (if not exceeding them then not dorsiventrally flattened), often with dorsal appendages 3.
3. Corolla white to cream with maroon to brown spots 4.
4. Lower dorsal horn of inner corona lobe considerably longer than half length of upper horn, pedicel (15-) 30-60 mm long 7. *O. albocastanea*
4. Dorsal horn of inner corona lobe < half length of upper horn, pedicel 10-15 mm long 8. *O. knobellii*
3. Corolla yellow to red or blackish or spotted with yellow on maroon but not white to cream with dark spots 5.
5. Inner corona lobes at most equalling anthers, with terete to strongly laterally flattened recurved horn just behind apex (apex often present only as slight swelling beneath this horn) 6.
6. Inner corona lobes excavated or furrowed near base with ridges and crests $\pm$ in series with outer lobes 6. *O. melanantha*
6. Inner corona lobes neither excavated nor furrowed near base (with 2 $\pm$ erect to recurved dorsal horns somewhat above base) 9. *O. lutea*
5. Inner corona lobes much exceeding anthers and dorsiventrally flattened to nearly terete beyond them 7.
7. Corolla lobes flat above, inner corona lobes with stout dorsal horn around middle, corona completely contained within corolla tube 10. *O. gerstneri*
7. Corolla lobes distinctly convex above, inner corona lobes gibbous and/or crested towards base only, tips of lobes often protruding from corolla tube 8.
8. Corolla 35-45 mm diam 12. *O. valida*
8. Corolla 55-85 mm diam 11. *O. huillensis*
1. Inflorescence with 1-3 flowers opening in gradual succession 9.
9. Stems wholly prostrate or, if ascending, then soon arching back to ground and becoming prostrate, inner corona lobes tuberculate or papillate 10.
10. Outer corona lobes bifid, thickened and irregularly tuberculate towards apex, inner lobes irregularly tuberculate but not papillate ('hairy') 28. *O. longii*
10. Outer corona not as above, inner corona lobes papillate ('hairy') 11.
11. Corolla prominently bicampanulate, lobes deltate and acute, smooth inside, inner corona lobes not rising significantly above anthers 29. *O. conjuncta*
11. Corolla rotate to very shallowly bicampanulate, lobes ovate and acuminate, papillate inside, inner corona lobes rising above anthers and diverging towards tips 30. *O. hardyi*
9. Stems $\pm$ erect at least in upper half, inner corona lobes smooth 12.
12. Inflorescences usually several per stem arranged along sides of stem especially towards apex 13.
13. Corolla 6-20 mm diam 14.
14. Corolla campanulate, outer corona forming urceolate cup around anthers 3. *O. carnosa*
14. Corolla $\pm$ rotate, outer corona not urceolate, lobes spreading $\pm$ horizontally and forming continuous flat and spreading pentagonal disc-like structure around gynostegium (often finely toothed along margin) broadest opposite inner lobes 1. *O. schweinfurthii*
13. Corolla 25-45 mm diam 15.
15. Corolla lobes with clavate marginal cilia near bases, inner corona lobes bifid into slender terete filiform lobules 7-9 mm long and entangled with similarly filiform dorsal projection above gynostegium 23. *O. rogersii*
15. Corolla lobes without marginal cilia, inner corona lobes 4-5 mm long, not bifid, slender but not filiform, connivent in narrow column above gynostegium 2. *O. lugardii*
12. Inflorescence 1 per stem near base 16.
16. Corolla with ring-like annulus surrounding but not supporting corona 17.
17. Inside of corolla smooth, corolla campanulate, 18-32 mm diam 19. *O. paradoxa*
17. Inside of corolla rugulose or verrucose, corolla rotate to shallowly bowl-shaped, (30-) 45-110 mm diam 18.
18. Annulus prominent, forming tube in centre of corolla 19.
19. Corolla with very prominent $\pm$ erectly tubular annulus more than twice as tall as gynostegium, margins of corolla lobes with prominent vibratile clavate cilia 13. *O. ciliata*
19. Corolla with spreading to recurved annulus much shorter than gynostegium, margins of corolla lobes eciliate or with short rigid cilia 20.
20. Outer corona lobes acute, inner lobes without prominent dorsal horn 26. *O. namaquensis*
20. Outer corona lobes linear-oblong with 2-3-toothed apex, inner lobes with prominent dorsal horn 27. *O. variegata*
18. Annulus insignificant, forming thickening on side of shallow corolla tube 21.
21. Inner corona lobes with fairly prominent knob-like dorsal horn 24. *O. pulchella*
21. Inner corona lobes without dorsal horn 25. *O. verrucosa*
16. Corolla with dome-like or cushion-like annulus supporting and beneath corona 22.

(Continued on next page)

Key to the species (continued)

22. Corolla 10–18 mm diam., stems uniformly coloured	4. <i>O. miscella</i>
22. Corolla 22–75 mm diam., stems mottled with purple on green	23.
23. Outer corona continuous and disc-like around gynostegium, forming horizontal platform below guide-rails and much swollen ± rectangular ridge rising up to meet inner lobes	18. <i>O. maculata</i>
23. Outer corona consisting of 5 discrete lobes beneath guide-rails, not spreading and disc-like around gynostegium	24.
24. Inner corona lobes much exceeding anthers to become erect beyond them, usually terete and ± clavate towards apices	25.
25. Inside of corolla conspicuously rugulose	26.
26. Tubercles on stems 4–7 mm long, inner corona lobes 2.0–3.5 mm long	20. <i>O. cooperi</i>
26. Tubercles on stems 10–25 mm long, inner corona lobes 4–5 mm long	21. <i>O. tapscottii</i>
25. Inside of corolla only faintly rugulose or smooth	27.
27. Corolla lobes strongly reflexed, margins of lobes with fine rigid cilia, inner corona lobes clearly clavate and tuberculate towards tips	22. <i>O. umbracula</i>
27. Corolla lobes spreading and corolla ± rotate, margins of lobes with vibratile clavate to spatulate cilia, inner corona lobes at most slightly clavate and tuberculate towards tips (usually neither)	14. <i>O. halipedicola</i>
24. Inner corona lobes dorsiventrally flattened and only slightly exceeding anthers, rarely becoming erect and never ± terete and clavate beyond them	28.
28. Corolla with shallow tube with corona seated on small abruptly raised annulus (± twice as tall as thick) at base of tube	17. <i>O. longidens</i>
28. Corolla tube formed entirely by annulus, annulus at most as tall as thick	29.
29. Corolla inside smooth, annulus widening towards surface of corolla	16. <i>O. maccloughlinii</i>
29. Corolla inside rugulose at least on lobes; annulus at least slightly constricted towards base	15. <i>O. woodii</i>

short peduncle (rarely up to 15 mm long), with 1–several lanceolate bracts 1–8 mm long often with lateral teeth; *pedicel* (1–) 3–50 (–55) mm long, 1.5–4.0 (–5.0) mm thick, mostly spreading (rarely erect); *sepals* 3–8 mm long, 1.5–4.0 mm broad at base, lanceolate, acuminate. *Corolla* rotate to campanulate (rarely bicampanulate), often strongly thickened below bases of lobes into prominent (occasionally broadly funnel-shaped) annulus around mouth of tube, (9–) 10–100 (–110) mm diam., mostly deeply lobed; outside glabrous and smooth, often streaked with purple; inside deeply reticulately rugulose to ± smooth, rarely with obtuse multicellular papillae, often with individual cells projecting as papillae; *tube* 1–6 (–12) mm deep, mostly shallowly bowl-shaped to ± absent, occasionally formed entirely by annulus (with corolla ± flat); *lobes* spreading to reflexed, (3–) 10–28 (–35) mm long, (2–) 4–25 mm broad at base, deltate, acute, ± flat above, margins often with vibratile clavate cilia. *Corona* (1.5–) 3.0–7.0 mm tall, (2.5–) 4.0–12.0 (–16.0) mm broad, consisting of 2 series arising on staminal tube, partly intergrown and not clearly separated from one another, glabrous (rarely papillate-pubescent), usually raised above base of tube on pentagonal stipe up to 3 mm long; outer *lobes* often consisting of 5 discrete spreading to erect ± subquadrate lobes beneath the guide-rails (rarely much reduced) often spreading around gynostegium behind anthers, often with erect lobule towards base enclosing small nectarial cavity; inner *lobes* adpressed to backs of anthers, often exceeding them and rising connivent in centre, dorsiventrally flattened towards base, becoming terete above, often with laterally flattened fin-like dorsal appendage. *Anthers* horizontal on top of style-head, margins often not shrinking back and frequently covering pollinia, rectangular to semicircular. *Pollinium* ± D-shaped, insertion-crest twisting from outer edge onto dorsal surface, caudicle attached with broad cupular pad to base. *Follicles* 50–150 mm long, erect, terete-fusiform, obclavate, slender, consisting of 2 horns diverging at 30–60°, longitudinally mottled with narrow broken purple stripes, glabrous, smooth.

In the new sense, the genus *Orbea* is characterised especially by features of the stems. Although the stems are very variable in size, in the manner in which they are grouped together and especially in the extent to which they are rhizomatous, they all share a relatively smooth, non-papillate surface (however, see *O. longii*, where the stems are somewhat papillate) with tubercles which taper gradually to their tips without any well-defined leaf (its base often only being demarcated by the presence of two small stipular denticles). In almost all of them (the only exception being *O. miscella*), the stems are brightly mottled with purple on various shades of green, especially if they are exposed to the sun. By the nature of its leaf-rudiments and the surface of the stems, the genus is readily separated from *Stapelia*, *Tridentea* and *Tromotriche* but the stems are actually very similar to those in species of *Duvalia* and *Huernia*.

Within the flower there are, however, substantial but fairly cryptic differences between *Duvalia* and *Huernia* and *Orbea* and in these features *Orbea* is similar to *Stapelia*, *Tridentea* and *Tromotriche*. In *Duvalia* and *Huernia* the inner and outer coronas are well separated on the gynostegium, the base of the gynostegium has a stipe with a circular cross-section (if there is one at all – if it is lacking, the outer corona lobes are somewhat fused to the base of the corolla tube) and the pollinia are elliptical and longer than broad with the insertion-crest exactly down the outer edge. The corpuscle to which they are joined is stout and at most slightly longer than broad. In *Orbea*, on the other hand, the inner and outer coronas are intergrown and are not separated on the gynostegium, the stipe is pentagonal

in cross-section (in the few cases where it is lacking the corona is not at all fused to the corolla tube and traces of its pentagonal shape are still visible up the sides of the gynostegium), while the pollinia are D-shaped and have their insertion-crest twisted from the outer edge onto the dorsal surface. The corpuscle is generally much longer than broad.

Orbea is a very widely distributed genus of 56 species. There are slightly more species in the southern African region than in the parts north of the equator (see Table 2). North of the equator there is one species (*O. decaisneana*) which is found from coastal West Africa to the Sudan, there are several species in the arid parts of north-eastern Africa and five which are endemic to south-western and southern Arabia, from Saudi Arabia to Dhofar in Oman. The largest number of species in the north-east is found in Ethiopia and Kenya (Table 4). Perhaps most unusual is the wide distribution of *O. schweinfurthii*, which is found from Uganda southwards to northern Namibia, Botswana and western Zimbabwe, to some extent following the Rift Valley. This pan-equatorial distribution, which connects up the north-eastern and southern centres of stapeliad-diversity (Bruyns 2000b), is unique among the stapeliads.

In southern Africa *Orbea* exhibits the opposite tendency to the stapeliads as a whole, with higher concentrations predominating along the eastern side of the subcontinent (fig. 10.1). For the stapeliads as a whole, high density was also detected in and around several mountain chains well away from the areas of maximum diversity. This pattern is repeated in *Orbea* in the Tiras Mountains and in the Great and Little Karas Mountains of Namibia, in the Blouberg and Soutpansberg

ORBEA SCHWEINFURTHII

of Limpopo Province, in the mountains along the Olifants River of Mpumalanga, and finally along the Lebombo Mountains which form the border between South Africa, Swaziland and Mozambique. For *Orbea* the highest number of species per half-degree square occurs along the northern flank of the Soutpansberg, where five species have been recorded. In contrast to genera such as *Quaqua* and *Tromotriche*, *Orbea* shows a marked lack of diversification in the arid parts of the winter-rainfall region of the Western Cape. Nowhere in this area is more than one species found per half-degree square. However, all of the species involved are derived taxa and this suggests that diversification in this region was relatively recent in *Orbea*.

1. *Orbea schweinfurthii*

Orbea schweinfurthii (A.Berger) Bruyns, *Aloe* 37: 76 (2001).

Caralluma schweinfurthii A.Berger, *Stap. u. Klein.*: 103 (1910).

Pachycymbium schweinfurthii (A.Berger)

M.G. Gilbert, *Bradleya* 8: 23 (1990).

Angolluma schweinfurthii (A.Berger) Plowes, *Excelsa* 16:18 (1994).

Type: Zaire, Ruthuru plains south-west of Lake Edward, at Nswiwa, Itande, 9 April 1891, 880 m, Stuhlmann 2208 (NY).

Caralluma piarantoides Obermeyer, *Fl. Pl. South Africa* 15: t. 599 (1935).

Type: Zimbabwe, Wankie distr., Levy 8444 (PRE).

Small succulent forming diffuse mat up to 1 m or more in diam., not rhizomatous. Stems 30-150 mm long, 4-12 mm thick (excluding teeth, sometimes more slender towards base), slender, decumbent (usually prostrate in lower half then ascending towards apex, rarely erect), branching from base to near apex, green to red mottled with purple-brown; *tubercles* (3-) 5-25 mm long, arranged very loosely into 4 obtuse rows along stem (stem $\pm$ cylindrical in cross-section when turgid) with slight groove between rows, tapering into prominent slender conical (sometimes laterally flattened) spreading tooth, tooth sometimes with 2 small denticles near apex, slightly flattened above towards apex. *Inflorescences* 1-4 per stem around apex and close to axils of neighbouring tubercles, each of 1-3 (-8) flowers developing in gradual succession from short (< 1 mm long) peduncle; *pedicels* 2-4 mm long, 1 mm thick, erect, with small often toothed $\pm$ rectangular bracts < 1 mm long at and near base; *sepals*



Fig. 10.3. Distribution of *Orbea schweinfurthii*.

2-3 mm long, 1 mm broad at base, ovate-lanceolate, acuminate. *Corolla* 10-15 mm diam., rotate; outside pale grey-green with maroon spots towards base; inside deep yellow with dark maroon spots becoming solid towards tips of lobes, densely papillate but not rugulose; *tube* < 0.5 mm long, formed by thickening of corolla below sinuses of lobes into slight pentagonal cushion-like annulus beneath outer corona lobes; *lobes* $\pm$ 3.0-3.5 mm long, 3 mm broad at base, spreading, ovate-deltate, acute, with reflexed tips, lightly convex above from slightly reflexed margins. *Corona* $\pm$ 2 mm tall, 7 mm broad, raised to level of mouth of tube on cylindrical stipe $\pm$ 0.5 mm long, pale yellow to cream speckled with purple; *outer lobes*

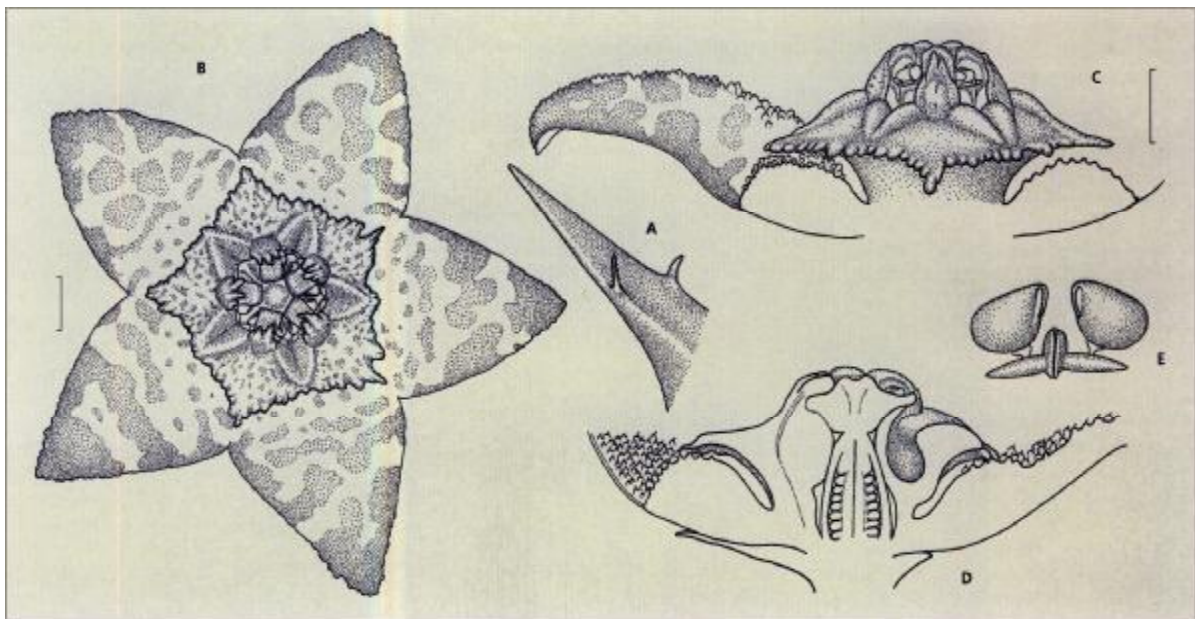


Fig. 10.4. *Orbea schweinfurthii*. A, apex of tubercle with stipular denticles. B, face view of flower. C, side view of centre of dissected flower. D, half-flower. E, pollinarium. Scale bars: A, C, D, 1 mm (at C); B, 1 mm; E, 0.25 mm (at C). Drawn from: PVB 2289, Bukalo, south-west of Katima Mulilo, Namibia.

horizontally spreading and fused together laterally to form continuous flat pentagonal disc-like structure (with corners opposite anthers, 1.5 mm broad from bases of inner lobes) around gynostegium with many-toothed to entire margin, with broad groove beneath each guide-rail; *inner lobes* $\pm$ 0.5 mm long, adpressed to backs of anthers and about half as long as them, $\pm$ deltoid, usually with 1-4 short obtuse apical teeth, dorsiventrally flattened.

Distribution and habitat

This extremely widely distributed species is found over a broader area outside southern Africa than within it. It is known from Central and East Africa where it occurs in the Congo, Rwanda, Zimbabwe, Tanzania, Uganda and Zambia (Leach & Plowes 1966b). More recent exploration has detected it in Malawi around Lake Malawi (Hargreaves 1979), in Botswana in the Okavango Delta and in the Caprivi Strip of Namibia. I have also found it to be fairly widespread in central Tanzania.

In southern Africa *O. schweinfurthii* usually grows in low-lying (but above 450 m), flat areas which, during the rainy season, become extremely wet, often with scattered pools of standing water. It is usually found in *mopane* woodland under small bushes or in the open alongside trees, sometimes in sandy soils but sometimes in quite muddy or loamy areas. However, in Tanzania its habitat seems to be remarkably variable. Here it is sometimes associated with dense *Acacia-Euphorbia-Monadenium* scrub (as in the gorge of the Great Ruaha River), sometimes with *Acacia-Commiphora-Balanites* scrub. It was also observed on a few occasions in dry *Brachystegia* woodland or even among quartz pebbles and larger rocks at altitudes of up to 2000 m near Mbulu.

Diagnostic features and relationships

Plants of *O. schweinfurthii* may form diffuse clumps as large as 1 m in diameter but the stems do not exhibit any significant tendency to spread underground and are never rhizomatous. They have a very loosely spreading, pronouncedly decumbent or 'semi-trailing' habit: in many stems the lower half is prostrate (sometimes becoming slightly subterranean) and only towards the apex does it begin to ascend. Many of the stems also have relatively few pairs of tubercles so that in a stem 60 mm long there are often only 4-6 pairs of tubercles and these are especially widely spaced towards the base. The tubercles are comparatively large and each is tipped with a tooth (slightly flattened above) which often bears a pair of small denticles at its base.

The tiny, more or less flat flowers are produced in several small inflorescences near the tips of the stems. Despite their small size, they are very strikingly and prettily coloured. Usu-



Fig. 10.5. *O. schweinfurthii*, PVB 8732, south of Dodoma, Tanzania.

ally the corolla is mottled inside with maroon on a deep yellow background with the maroon coalescing towards the tips of the lobes and it is covered quite densely with multicellular papillae. The flowers emit a fruity, sweetish odour (Agnew 1976).

The corona is similarly speckled with purple on a slightly paler yellow to cream background and is often shiny with nectar which is secreted over most of its surface. The shape of this corona is unique and most distinctive. It consists of a pentagonal disc, spreading just above the surface of the flower, which has been shown to arise entirely from what are initially five discrete outer corona lobes. This outer disc is broadest opposite the anthers and has five grooves beneath the guide-rails leading, in fact, to a fairly deep nectarial cavity beneath the

rails. Its edges are usually toothed all the way around. The inner corona lobes rise from this disc and partly cover the backs of the anthers, remaining small and insignificant.

Although the stems and inflorescences of *O. schweinfurthii* are very typical of *Orbea*, especially of many of the 'northern' species, the flowers are particularly small. The very small pollinia are unusually broad and superficially resemble those of *Caralluma adscendens* but the wings on the corpuscle are differently shaped and the respective insertion-crests are differently oriented. Molecular data place *O. schweinfurthii* in a branch among the northern species of *Orbea* and they do not substantiate the position as sister to the rest of *Orbea* that was found in Bruyns (2002).



Fig. 10.6. *O. schweinfurthii*, PVB 7750, near Liwonde, Malawi, plants spreading among dried leaves on the floor of *Colophospermum mopane* 'forest'.

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Fig. 10.7. *O. schweinfurthii*, PVB 2289, Bukalo, south-west of Katima Mulilo, Namibia.



Fig. 10.8. *O. schweinfurthii*, PVB 6510, north of Maun, Botswana.

History

Orbea schweinfurthii was discovered by F. Stuhlmann on 9 April 1891 on the eastern border of the Congo near Vitschumbi on the plains north of Rutshuru. This lies just south of Lake Edward and is an area where it seems to be quite common, for several records have been made in the vicinity. The original collection was made during the last expedition into the interior of Central Africa (1890-92) of the Emin Pasha (the German explorer and adventurer Eduard Schnitzer, who had converted to Islam and assumed this name). It was named by Alwyn Berger for the German scientist and explorer Georg August Schweinfurth, in whose herbarium Stuhlmann's specimen was preserved, though this specimen was subsequently lost during the bombing of Berlin during World War II. A lectotype was selected in Bruyns (2002) but the discovery of some of the type collection in the New York Botanical Garden Herbarium (NY) renders this superfluous. As shown by Leach & Plowes (1966b), Berger was most probably wrong in the locality that he gave for Stuhlmann's collection.

Caralluma piaranthoides was described from material discovered by Benjamin Levy (see under *Huernia levyi*) in about 1933 near Hwange (Wankie) in Zimbabwe. Berger's illustration makes it clear that *C. piaranthoides* is a synonym of *O. schweinfurthii* and this was first realised by Leach & Plowes (1966b).

2. *Orbea lugardii*

Orbea lugardii (N.E. Br.) Bruyns, *Aloe* 37: 75 (2001).
Caralluma lugardii N.E. Br., *Fl. Trop. Afr.* 4 (1): 487 (1903).
Pachycymbium lugardii (N.E. Br.) M.G. Gilbert, *Bradleya* 8: 28 (1990).
Angolluma lugardii (N.E. Br.) Plowes, *Excelsa* 16: 120 (1994).
 Type: Botswana, Totin (Toteng), near Lake Ngami, Lugard 74 (K).
Caralluma longicuspis N.E. Br., *Fl. Cap.* 4 (1): 884 (1909).
 Type: Namibia, sub N.S. Pillans 14 (BOL).

Small succulent usually consisting of several clumps 60-500 mm dia. connected by $\pm$ horizontal rhizomes. Stems 40-150 mm long, 6-12 mm thick (excluding teeth), erect often with subterranean base (to 100 mm long or more and 4-8 mm thick), pale green to silvery grey flecked with purple-brown mainly down grooves between angles; tubercles 3-5 mm long, arranged in and partly joined into 4 obtuse angles along stem with groove between angles, tapering into conical spreading acuminate tooth somewhat flattened above and slightly laterally expanded at the base. Inflorescences 2-6 per stem usually in upper half or near apex, each of 1-3 (-7) extremely smelly flowers developing in gradual succession (sometimes all opening simultaneously) from short peduncular swelling; pedicel 3-6 mm long, 1.0-1.5 mm thick, ascending and usually holding flower facing upwards, with few broadly ovate acute bracts 1-2 mm long at base; sepals 3-5 mm long, 1.0-1.5 mm broad at base, lanceolate, acuminate. Corolla 30-45 mm diam., campanulate to rotate, very deeply and narrowly lobed; outside smooth and pale green; inside not rugulose but finely papillate all over and very variably coloured usually with lobes paler than centre (yellow-green, yellow, red, brown with red or brown centre); tube 3-6 mm long, 5-8 mm broad, bowl-shaped, corolla only



Fig. 10.9. *O. lugardii*, PVB 6506, north of Maun, Botswana. Two cuttings showing the white, underground shoots from which they arose.

very slightly thickened towards mouth, containing gyno-stegium except for tips of inner corona lobes; lobes 18-25 mm long, 3-4 mm broad at base, shortly deltate towards base then slenderly attenuate, acuminate, spreading, with minute rigid cilia along recurved margins. Corona $\pm$ 6 mm tall, 4.5-6.0 mm broad, raised above base of tube on short stout pentagonal stipe (< 0.5 mm long), glabrous; outer lobes 1-2 mm long, ascending, deeply bifid into narrow elongated-deltoid acute diverging lobules, red to purple-brown; inner lobes 4-5 mm long, adpressed to backs of anthers then connivent-erect and sometimes diverging at apices, dorsiventrally flattened, linear from narrowly ovate base, reddish around base to yellow above, with few small ridges on rear above longer square emarginate spreading gibbosity laterally fused to and in series with outer lobes.



Fig. 10.10. *O. lugardii*, PVB 6469, Kuke, Botswana, in habitat, December 1995.

Distribution and habitat

Orbea lugardii has been surprisingly rarely collected and there were only a few records of it in southern African herbaria. However, a concerted effort to record it wherever it was encountered has revealed it to be widely distributed over much of southern Africa.

This collecting has shown that it is of almost universal occurrence in Namibia, except in the winter-rainfall area south of Helmeringhausen, the arid Namib Desert along the coast, in the sands of the relatively moist Ovamboland and in the Caprivi. In Botswana it is mainly found in the west (probably more widely towards the south than the existing records show) and in the central parts of the Okavango Delta. In South Africa it is found in two areas. One is in the region from Upington and Kimberley northwards into the Kalahari and the other lies in the extreme northern corner of the country north of the Soutpansberg. From here there is only a single record and it may prove to be more widespread in this area. White & Sloane (1937: 387) also mention its probable occurrence in Zimbabwe but this has not been confirmed by any records. It remains a possibility also that it might occur in southern Angola.

In general *O. lugardii* is a plant of dry (but not desertic) areas and grows under small bushes such as *Rhigozum trichotomum*, *Monechma cleomoides* or *Blepharis* or among trees (often *Acacia* or *Colophospermum*



Fig. 10.11. *O. lugardii*, PVB 3649, south of Prieska.

mopane). Specimens are usually scattered and often not easy to see but, in overgrazed conditions, they can become large (up to 500 mm in diameter) and very common indeed. They have a particular predilection for areas underlain by calcrete and often grow where this is covered by a thin layer of sand.

There are several other species with broad, central southern African distributions such as this one - e.g. *Duvalia polita*, *Piранthus decipiens*, *Orbea lutea* and *Tavaresia barklyi*. However, the distribution of none of these species is very similar to that of *O. lugardii*, which is broader than any of these except *D. polita*.

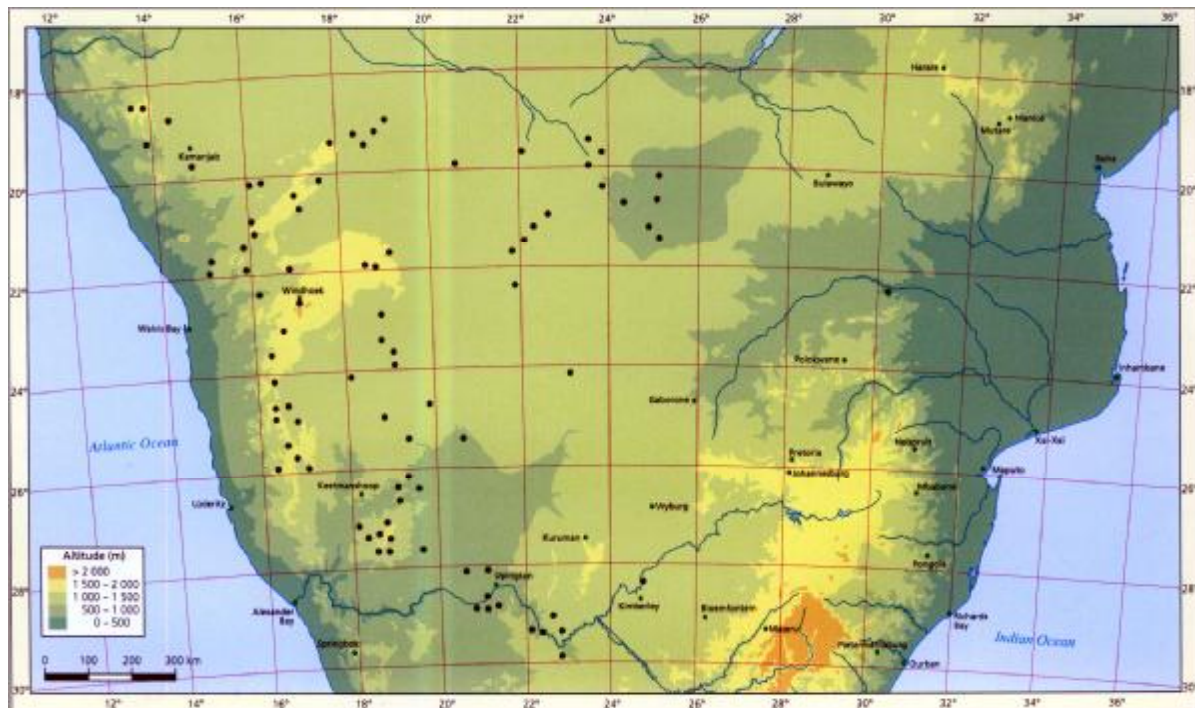


Fig. 10.12. Distribution of *Orbea lugardii*.

Diagnostic features and relationships

Most plants of *O. lugardii* are small (often only 40–60 mm in diameter), but they are extremely rhizomatous and may consist of several clumps of stems (sometimes only single stems) connected under the surface by slender runners. As is usual, where these runners emerge from the soil, they become thicker. However, the stems of *O. lugardii* are never very thick (they are mostly 8–10 mm in diameter but a maximum of about 12 mm is sometimes achieved) and they have low, obtuse angles from which the tubercles do not project significantly. They are generally greyish, flecked with purple-brown mainly down the grooves between the angles.

Each tubercle is tipped in the beginning with a spreading tooth which is a little flattened above and has a broadened base tapering to a slender tip. This soon wears off. The colour and shape of the stems is reminiscent of that in *Tridentea* and the leaves are also superficially like those in *Tridentea*, though actually they are flatter and they lack the marginal hairs typical of *Tridentea*. As in all species of *Tridentea* and in several other species of *Orbea*, the stems of *O. lugardii* are edible.

In this species flowers are produced in several small inflorescences towards the apices of the stems. If conditions are favourable, often many are open simultaneously on a plant and a dreadful stench rather like that of horse-manure pervades the surroundings. The flowers are of

medium size when spread out fully, with very slender lobes and only a small, central, united and shallowly bowl-shaped area. They are usually (but not always) bicoloured and are always without any spotting: most flowers are brown towards the centre, changing quite suddenly to a paler colour (often bright yellow) towards the tips of the lobes. The inner surface is finely velvety-papillate but not at all rugulose.

In *O. lugardii* the deeply bifid outer corona lobes are pressed laterally against the sides of the broad dorsal appendages of the inner lobes so that altogether there is an almost continuous cupular structure containing the centre of the gynostegium. The inner lobes are adpressed to the anthers and then rise up in a long, slender column in the centre. They are usually yellow

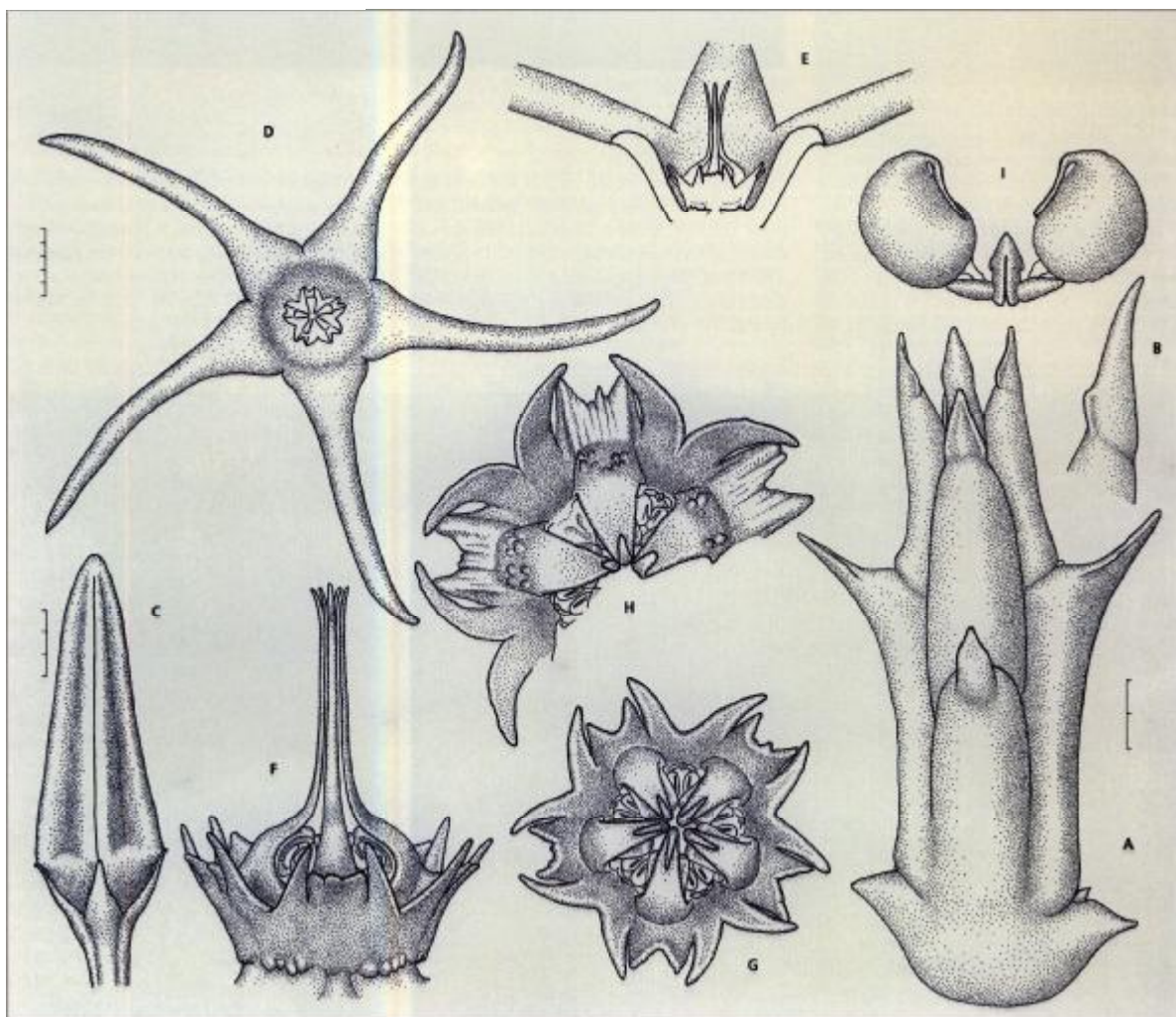


Fig. 10.13. *Orbea lugardii*. A, apex of stem. B, apex of tubercle with stipular ridge. C, bud. D, face view of flower. E, side view of centre of dissected flower. F, side view of gynostegium. G, H, face view of gynostegium. I, pollinarium. Scale bars: A, 2 mm; B, F, G, H, 1 mm (at A); C, E, 3 mm (at C); D, 5 mm; I, 0.25 mm (at A). Note that G and H are drawn to the same scale! Drawn from: A, C–G, I, PVB 2328, Tsumeb, Namibia (no specimen); B, H, PVB 3282, Kloof, Prieska.



Fig. 10.14. *O. lugardii*, PVB 1950, near Steinhausen, Namibia.

(sometimes with reddish margins) and are paler than the outer series.

Morphological data indicate that *O. lugardii* is most closely allied to *O. ubomboensis*, with which it shares the manner in which the flowers are produced towards the top of the stems, the rhizomatous habit and the papillae on the inside of the corolla (Bruyns 2002). However, molecular data does not substantiate this and places *O. lugardii* together with *O. carnosa* and *O. gerstneri*.

History

In Namibia, where it is probably most widespread, *O. lugardii* was first recorded from Damaraland by Ture Johan Gustav Eén in 1879 (BM records). Material was collected, probably between 1896 and 1899, at Toteng (Totin), southwest of Maun in north-western Botswana by Edward J. Lugard and it was from this material that N.E. Brown described *Caralluma lugardii* in 1903.



Fig. 10.15. *O. lugardii*, PVB 6469, Kuke, Botswana, covered in flowers, in especially overgrazed area, December 1995.

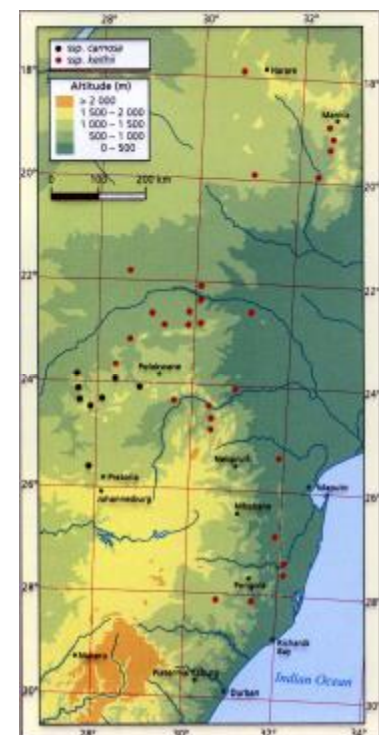
3. *Orbea carnosa*

Orbea carnosa (Stent) Bruyns, *Aloe* 37: 73 (2000).
Caralluma carnosa Stent, *Bull. Misc. Inform.* 1916: 42 (1916).

Pachycymbium carnosum (Stent) L.C. Leach, *Excelsa Taxon. Ser.* 1:7(1978).

Type: South Africa, Transvaal, Zilikaat's Nek, Pole Evans 11020 (PRE).

Dwarf succulent usually consisting of several small clumps connected by $\pm$ horizontal rhizomes, sometimes forming dense to diffuse clumps 60-500 mm diam. Stems 40-150 mm long, 10-20 mm thick (excluding teeth), stout, erect to spreading from shortly horizontal to extensively subterranean base, grey-green to reddish mottled with red to purple; tubercles (6-) 10-15 mm long, joined into 4 narrowly obtuse continuous wing-like rows along stem with deep groove between rows, laterally flattened, forming spreading to slightly decurved acute broadly to narrowly deltoid tooth usually with pair of small denticles near apex. Inflorescences 1-6 (-10) per stem mainly in upper half, each with 1-2 (-3) flowers developing in rapid succession, with 1-3 lanceolate acute bracts 1-2 mm long; pedice/(1-)2-6(-12) mm long, 1-2 mm thick, spreading to descending so flower often nodding; sepals 2.5-5.0 mm long, 1.0-1.5 mm broad at base, ovate to lanceolate, acuminate. Corolla 6-20 mm diam., campanulate, fleshy (0.5-1.5 mm thick in tube); outside pale green spotted with purple to uniformly pink or cream; inside irregularly



ORBEA CARNOSA

Key to the subspecies of *O. carnosa*

Corolla 6–10 mm diam., lobes 2–5 mm broad	3a. subsp. <i>carnosa</i>
Corolla 10–20 mm diam., lobes 6–8 mm broad	3b. subsp. <i>keithii</i>

rugulose, with scattered erect spike-like papillae up to 1 mm long, uniformly yellow or maroon to pale brown or maroon with irregular reticulated cream markings or whitish with dark purple flecks; *tube* 2.5–4.0 mm long, 4–7 mm broad, cupular, pentagonal, mouth constricted by inward-pointing annulus, nearly to completely containing gynostegium; *lobes* 3–5 mm long, 6–8 mm broad at base, deltate-ovate, acute, rigidly spreading to ascending, with spreading fold in each sinus and few small rigid clavate cilia up to 1 mm long along margin near base. *Corona* 3–4 mm tall, 4 mm broad, cream with purple-red patches, with very short stipe or sessile; *outer lobes* erect then spreading, spreading part entire and truncate-emarginate to deeply bifid into narrowly deltoid lobules, fused laterally $\pm$ in middle to inner lobes to form urceolate cup exceeding anthers, channelled along middle; *inner lobes* $\pm$ 1 mm long, adpressed to backs of anthers and slightly exceeding them, $\pm$ linear, truncate to acute, often very thick, with thick obtuse dorsal gibbosity.

The main differences listed by Leach & Plowes (1967) between *Caralluma carnosa* and *C. keithii* were: corolla 6–10 mm diam. in *C. carnosa*, 10–20 mm in *C. keithii*; corolla white to buff with brown to maroon markings in *C. carnosa*, always deep maroon, with or without markings in *C. keithii*; pollinia 0.4 x 0.25 mm in *C. carnosa*, c. 0.6 x 0.4–0.5 mm in *C. keithii*. Since '*keithii*' has been found with pale brown and even yellow flowers ('*lancasteri*') and occasional reddish flowers of '*carnosa*' have been seen, this distinction in their respective colours falls away. Although the flowers of *C. carnosa* are often smaller, there is no discontinuity in the size of the flowers either. There is some difference in the shape of the respective pollinia. These are more or less as broad as long in subsp. *keithii* and generally smaller and slightly longer than broad in subsp. *carnosa*. The two are distributed allopathically and so the rank of subspecies seems the most appropriate.



Fig. 10.20. *O. carnosa* subsp. *carnosa*, PVB 8751, Lapalala, Waterberg, a fairly large clump of stems at the base of a sandstone rock, January 2001.



Fig. 10.17. *O. carnosa* subsp. *carnosa*, PVB 6542, south of Ellisras.



Fig. 10.18. *O. carnosa* subsp. *carnosa*, PVB 6542, south of Ellisras.



Fig. 10.19. *O. carnosa* subsp. *carnosa*, PVB 6542, south of Ellisras, an especially dark-flowered plant.

3a. *Orbea carnosa* subsp. *carnosa*

*Pedice*l 1–3 mm long, 1 mm thick; *sepals* 2.5–4.0 mm long, 1 mm broad at base. *Corolla* 6–10 mm diam.; inside white-cream or greenish to brown with irregular (usually small) maroon to red markings; *lobes* 4–5 mm long, 2–5 mm broad at base, margins rarely with few small rigid cilia. *Corona* $\pm$ 2.0–2.5 mm tall, 3 mm broad.

Distribution and habitat

Subsp. *carnosa* is of fairly restricted distribution in northern South Africa from Pretoria and Rustenburg north-westwards to the Waterberg and west of this to near Ellisras.

This subspecies generally seems to be associated with sandstone mountains and hills, though plants have been seen on granite slabs near Potgietersrust. Specimens mainly grow under small bushes, in grass clumps or even among stones on exposed outcrops of rock with shallow pockets of soil. Rather more rarely they occur in open stony spots among trees.

Diagnostic features and relationships

Plants of subsp. *carnosa* are similar to those of subsp. *keithii*. They are very variably rhizomatous and some seen near Ellisras formed dense clumps up to 300 mm across, more or less without underground runners. These were growing in the flats at the foot of a hill, reasonably sheltered by trees. Those in more exposed situations are much more rhizomatous and usually consist only of small groups of stems connected by subterranean runners. The stems are boldly toothed as in subsp. *keithii* but they usually have a paler, grey-green background colour (with the usual purple mottling) and they may have slightly longer, narrower teeth.

The flowers of subsp. *carnosa* are usually considerably smaller than those of subsp. *keithii* and many are only 6–8 mm across. They are also much more variable in colour inside than those of subsp. *keithii*. Some very similar to what is typical for subsp. *keithii* are found, that is, with a brownish background speckled with white. However, most are almost pure white with numerous small maroon spots which become smaller in the tube below the annulus. Occasionally there is hardly any mottling at all. The corolla lobes usually ascend and only rarely do they spread out fully. The small tube is constricted at the mouth by a thickened ridge of tissue.

History

Subsp. *carnosa* was discovered by L.B. Pole-Evans a little before 1914 near the Hartebeespoort Dam at Zilikaat's Nek, which lies to the west of Pretoria in the Magaliesberg.

3b. *Orbea carnosa* subsp. *keithii*

Orbea carnosa subsp. *keithii* (R.A.Dyer) Bruyns,
Syst. Bot. Monogr. 63: 89 (2002).

Caralluma keithii R.A.Dyer, EL Pi. South Africa 15: t.
600 (1935).

Pachycymbium keithii (R.A.Dyer) L.C. Leach, Excelsa
Taxon. Ser. 1: 71 (1978).

Type: Swaziland, Lebombo Mountains, Keith sub
PRE 19790 (PRE).

Caralluma fosteri Pillans in A.C. White & B. Sloane,
Stap., ed. 2: 1292 (1937).

Type: Transvaal, Lydenburg distr., Foster sub BOL
213M (BOL).

Caralluma schweickerdtii Obermeyer, Bothalia 3: 250
(1937).

Type: Transvaal, between Waterpoort and Soutpan,
Obermeyer, Schweickerdt & Verdoom 411 (PRE).

Pachycymbium lancasteri Lavranos, Cact. Succ. J.
(US) 56: 196 (1984).

Type: South Africa, Kruger Park, Letaba distr.,
Percy-Lancaster 1431 (NBG).

Pedicele 2-6 (-12) mm long, 1.5-2.0 mm thick; *sepals*
3-5 mm long, 1.5 mm broad at base. *Corolla* 10-20 mm
diam.; inside uniformly yellow or maroon to pale brown or
maroon with irregular reticulated cream markings; *lobes*
3-5 mm long, 6-8 mm broad at base, margins commonly
with small rigid cilia. *Corona* 3-4 mm tall, 4 mm broad.

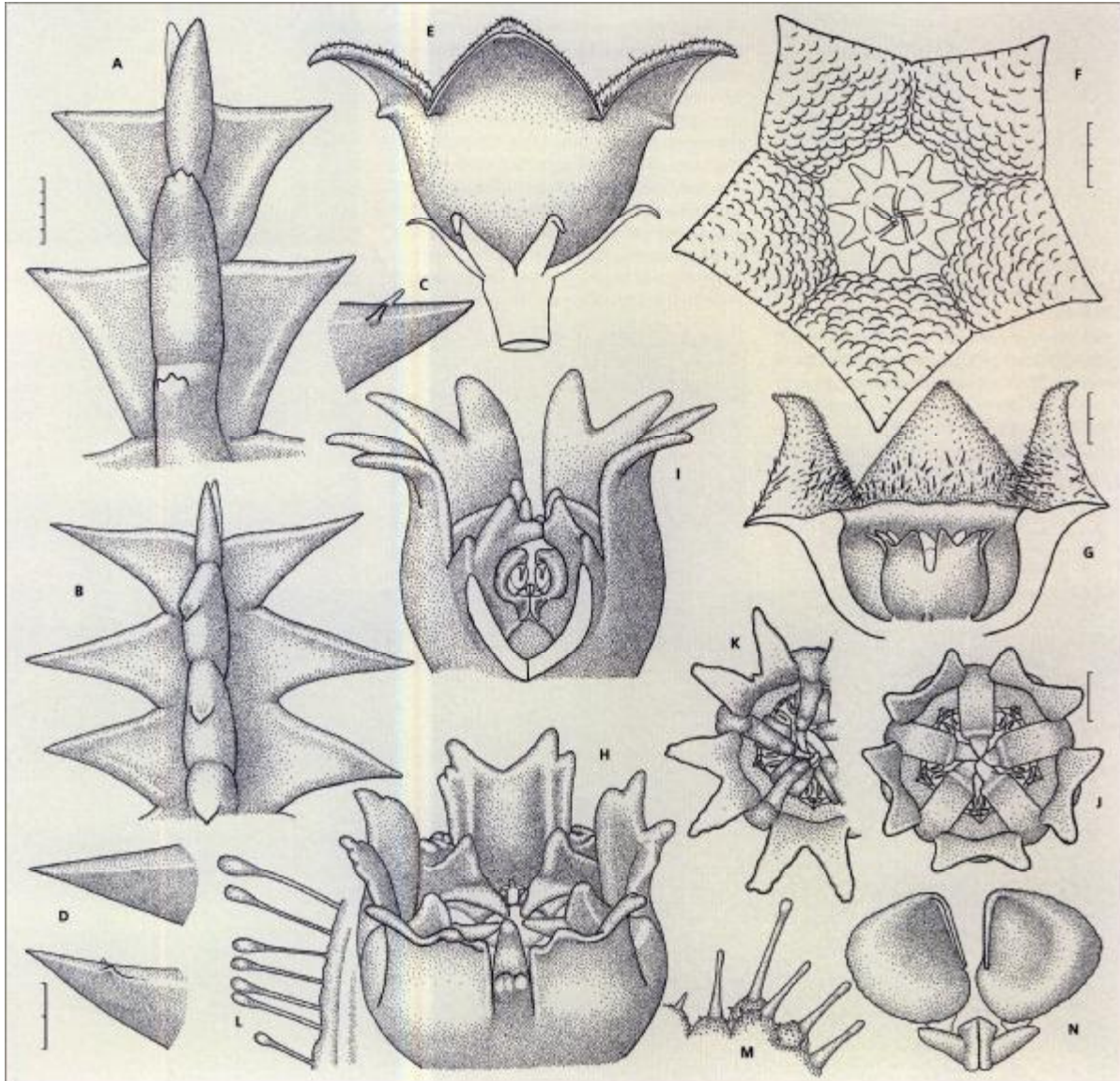


Fig. 10.21. *Orbea carnosa* subsp. *keithii*. **A, B**, apex of stem. **C, D**, apex of tubercle (both at D from same stem). **E**, side view of flower. **F**, face view of flower. **G**, side view of dissected flower. **H**, side view of gynostegium. **I**, side view of gynostegium with one outer corona lobe removed. **J, K**, face view of gynostegium (or part of it). **L**, papillae near base of lobe along margins, with interior of flower to right. **M**, papillae inside corolla around middle of lobe. **N**, pollinarium. Scale bars: **A, B**, 5 mm (at A); **C, D**, 2 mm (at D); **E, F**, 3 mm (at F); **G**, 2 mm; **H, I**, 1 mm (at D); **J, K**, 1 mm (at J); **L, M**, 0.5 mm (at D); **N**, 0.25 mm (at D). Drawn from: **A, C, H, L, M**, PVB 4453, Mkuzi; **B, D**, PVB 6558, Ga-Mankodi, south of Blouberg; **G, J**, PVB 2040, Penge; **E, F, I, K, N**, De Kock, Gutschwa Kop, near Nelspruit.

ORBEA CARNOSA

Distribution and habitat

Although it was described from plants found in Swaziland, subsp. *keithii* has been found over wide areas of the eastern parts of southern Africa.

In Zimbabwe it is known from various scattered records from Harare eastwards to Mutare and southwards to the vicinity of Beit Bridge. In South Africa it has been collected widely in the northern parts of the country especially north of the Soutpansberg, along the northeastern escarpment and in northern KwaZulu-Natal. It has been recorded in parts of Moçambique adjacent to the Lebombo Mountains of Swaziland and in the eastern corner of Botswana east of Selebi Phikwe (Hargreaves 1998).

Over this large area it is found in many different habitats. Generally it seems to grow in stony ground, usually in flat areas but sometimes it grows on slopes or even on the summits of hills. Plants may be found in the open among stones, in the shelter of small shrubs and grass tufts or alongside *Colophospermum mopane*, *Acacia* or even *Brachystegia* trees in soils derived from sandstones, igneous rocks or calcrete. They are occasionally found, too, on granite domes in shallow soils with clumps of *Selaginella* and the sedge *Coleochloa*.

Diagnostic features and relationships

Occasionally a specimen of subsp. *keithii* will form a large clump (up to 500 mm in diameter or more) but mostly small clusters of more

or less erect stems develop (over an area of 0.3-1.0m) which are connected by underground runners (as in fig. 10.23). As is usual, these runners are more or less cylindrical with small teeth along them. When they emerge from the ground, they become much thicker and develop very prominent tubercles. These tubercles are spreading to slightly recurved and very much laterally flattened. Along the stem they are joined into conspicuous, more or less continuous but often a little irregular wings. In the field the stems are usually strikingly mottled with red to purple on green.

As in subsp. *carnosa*, in subsp. *keithii* the flowers are produced in small groups, mainly towards the apices of the stems and often two are open at once on an inflorescence. They are small and campanulate, often with a nodding attitude and are noticeably thick and rigid, remaining open for up to a week and seeming to give off no noticeable scent. The lobes are very variable in the extent to which they open and it is only rarely that they spread out properly. While the outside is a nondescript cream to pink, inside they are strikingly coloured. Some flowers are plain yellow or red but usually there is a reticulated patterning of white on pale brown or maroon over the whole inner surface. The inside is also densely covered with an irregular reticulation of raised ridges. These are covered in a variety of papillae. The epidermal cells are spike-like and some are longer than others but also spike-like (fig. 29B). Others are very much larger and somewhat top-shaped (fig. 29 E, for subsp. *carnosa*). There is often a row of clavate hairs near the margins of the lobes near their bases



Fig. 10.22. *O. carnosa* subsp. *keithii*, Percy-Lancaster 1431, Kruger Park. An unusual plant with yellow flowers and a more prominent annulus than usual (photo: W.R. Liltved).

which are rigidly fixed and not at all vibratile. In the centre, containing the corona, is a small pentagonal tube around whose mouth the corolla is variably raised and thickened into an annulus. In plants found around Wyllie's Poort north of the Soutpansberg, the annulus can be practically absent to quite conspicuous and in the material described as *Pachycymbium lancasteri* there was a very obvious annulus.



Fig. 10.23. *O. carnosa* subsp. *keithii*, PVB 9378, near Nelspruit, very rhizomatous plant on granite dome in shallow peaty soil around the base of a plant of *Aloe petricola*.

The outer corona lobes rise steeply inside the corolla tube and much exceed the anthers. In many cases, towards its apex each lobe may be shallowly to deeply cleft into two spreading lobules. However, when the lobes are entire, they can be very similar to those in such species as *O. lutea* and they differ mainly in ascending steeply rather than spreading outwards. The inner lobes are extremely variable in shape. Usually each consists of a small lobe adpressed to the anther (mostly completely hiding and sometimes exceeding it) which is dorsally very much thickened and adorned with various small appendages. This thickened dorsal portion fills the gaps left between the outer lobes so that together they form the characteristic cup-like corona which contains the anthers and considerably restricts access to the guide-rails.

Pachycymbium lancasteri was described from a single plant which had yellow flowers, a more than usually prominent annulus and a conspicuously urceolate corona (fig. 10.22). Since pale brown flowers of subsp. *keithii* have

been seen, yellow could be viewed as a further variant in colour in subsp. *keithii*. The annulus, too, is very variably present in subsp. *keithii*. The outer corona is also very variable and Leach & Plowes (1967) mention an even more extreme case where it formed a 'crenulate margined, complete urceolate cup'. There seems no reason, therefore, not to consider *P. lancasteri* as falling within the range of variation of subsp. *keithii*.

History

Caralluma keithii was described from material collected by Donald Robert Keith (29 June 1896–4 March 1966) in about 1934 in the Lebombo Mountains some 20 miles south of Stegi (Siteki) in Swaziland. Keith was born in India and brought up at Hampton Court in London (in a 'grace and favour' apartment). After training at Sandhurst, he fought in World War I, was badly wounded in the Battle of the Somme (where he held the rank of captain in the Highland Light Infantry) and was awarded the Military



Fig. 10.24. Donald R. Keith, August 1926 (courtesy James H. Keith).



Fig. 10.25. *O. carnosa* subsp. *keithii*, PVB 6590, north-east of Wyllies Poort.



Fig. 10.26. *O. carnosa* subsp. *keithii*, PVB 6614, east of Burgersfort.



Fig. 10.27. *O. carnosa* subsp. *keithii*, PVB 4453, Mkuzi.

Cross. After recovering from his wounds, he went to an agricultural college in England and then became a farmer in Swaziland, where the climate was considered to be better for his health. His property, called Ravelston, lay on the summit of the Lebombo Mountains near Stegi and in it he had an extensive garden laid out, with a fine collection of Aloes and cycads. Before he became partially paralysed in 1939, he discovered several undescribed species in the area near his home and some, such as *Euphorbia keithii* and *Aloe keithii*, were named after him (James H. Keith, pers. comm. 2001).

It seems, though, that the first recorded collection of *Caralluma keithii* is one of Obermeyer, Schweickerdt and Verdoorn (described as *Caralluma schweickerdtii*) which was collected in November 1932 on the northern side of the Soutpansberg.

Leach & Plowes (1967) have indicated the confusion that has surrounded the names *Caralluma keithii* and *C. carnosa*. This was largely caused by the misidentification as *C. carnosa* of a plant collected near Waterpoort north of the Soutpansberg which came to be figured under that name in the *Flowering Plants of South Africa* (Phillips 1935a). This figure was reproduced in White & Sloane (1937) under the name '*carnosa*', so their view of the two 'species' was also muddled. This error was discussed for the first time in Verdoorn (1950) when the 'real' *C. carnosa* was figured and Lückhoff (1952) correctly identified *C. carnosa* and *C. keithii*. Leach & Plowes (1967) again clarified the position and established for the first time the synonymy of many of the names that had been published.

ORBEA MISCELLA

4. *Orbea miscella*

Orbea miscella (N.E. Br.) Meve, *Kakt. and. Sukk.* 5:186 (2000).

Stapelia miscella N.E. Br., *Fl. Cap.* 4 (1): 977 (1909).

Stultitia miscella (N.E. Br.) C.A. Luckh., 'S. A. G.' 29: 91 (1938).

Pachycymbium miscellum (N.E. Br.) M.G. Gilbert, *Bradleya* 8: 28 (1990).

Angolluma miscella (N.E. Br.) Plowes, *Excelsa* 16: 120 (1994).

Type: South Africa, Cape, near Klipplaat, *E. Pillans* sub N.S. Pillans 657 (K).

Caralluma bredae R.A. Dyer, *Fl. Pl. Africa* 36: t. 1438a (1964).

Type: Cape, Rietbron, *Van Breda* 708 (PRE).

Caralluma bredae var. *thomallae* R.A. Dyer, *Fl. Pl. Africa* 36: t. 1438b (1964).

Type: Cape, near Mortimer (?), *Thomalla* sub PRE 29286 (PRE).

Minute succulent forming several small clumps each 20-100 mm diam. connected by $\pm$ horizontal rhizomes. Stems above-ground 10-70 mm long, 4-8 mm thick, very slender, decumbent, sometimes running beneath surface for up to 150 mm, uniformly green to brown- or purple-green; *tubercles* 1-2 mm long, arranged in and partly joined into 4 obtuse angles along stem with groove between

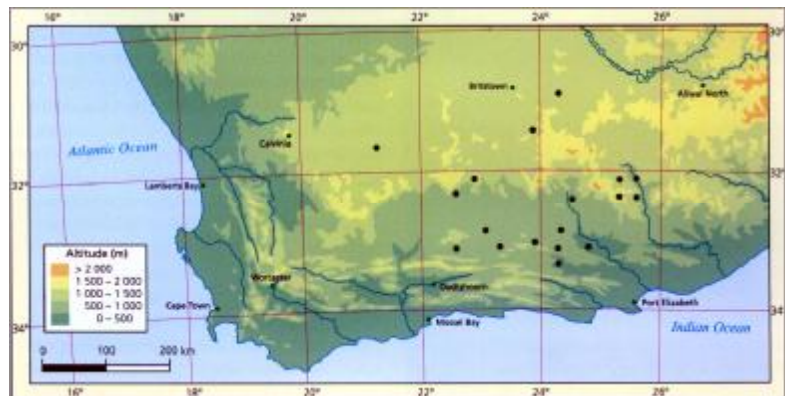


Fig. 10.28. Distribution of *Orbea miscella*.

angles, tapering into short spreading conical acute tooth, without stipular denticles. Inflorescence 1 (-2) per stem near base, of 1-3 flowers developing in gradual succession from short peduncle, with few lanceolate bracts 1-2 mm long; *pedicels* 4-18 mm long, 1.5 mm thick, erect holding flower facing upwards, flecked with brownish; *sepals* 2-3 mm long, 1 mm broad at base, ovate-lanceolate, acuminate. *Corolla* 10-18 mm diam, rotate, deeply lobed, usually evil-smelling; outside smooth, pale green; inside dark purple-brown, lightly to deeply reticulated

rugulose but not papillate; *tube* $\pm$ 1 mm deep, containing lower half of gynostegium, formed by thickened (0.5 mm) raised to incurved pentagonal annulus (sometimes divided into 5 raised $\pm$ isolated islands, 1 below each lobe); *lobes* 4-7 mm long, 2.5-3.0 mm broad at base, spreading to recurved, ovate-lanceolate to lanceolate, acuminate to acute, convex from reflexed margins, eciliate. *Corona* $\pm$ 3 mm tall, 2.5-1.5 mm broad, raised above base of tube on short pentagonal stipe (< 0.5 mm long), dark purple-brown to nearly black; *outer lobes* $\pm$ 0.5 mm long, 1 mm

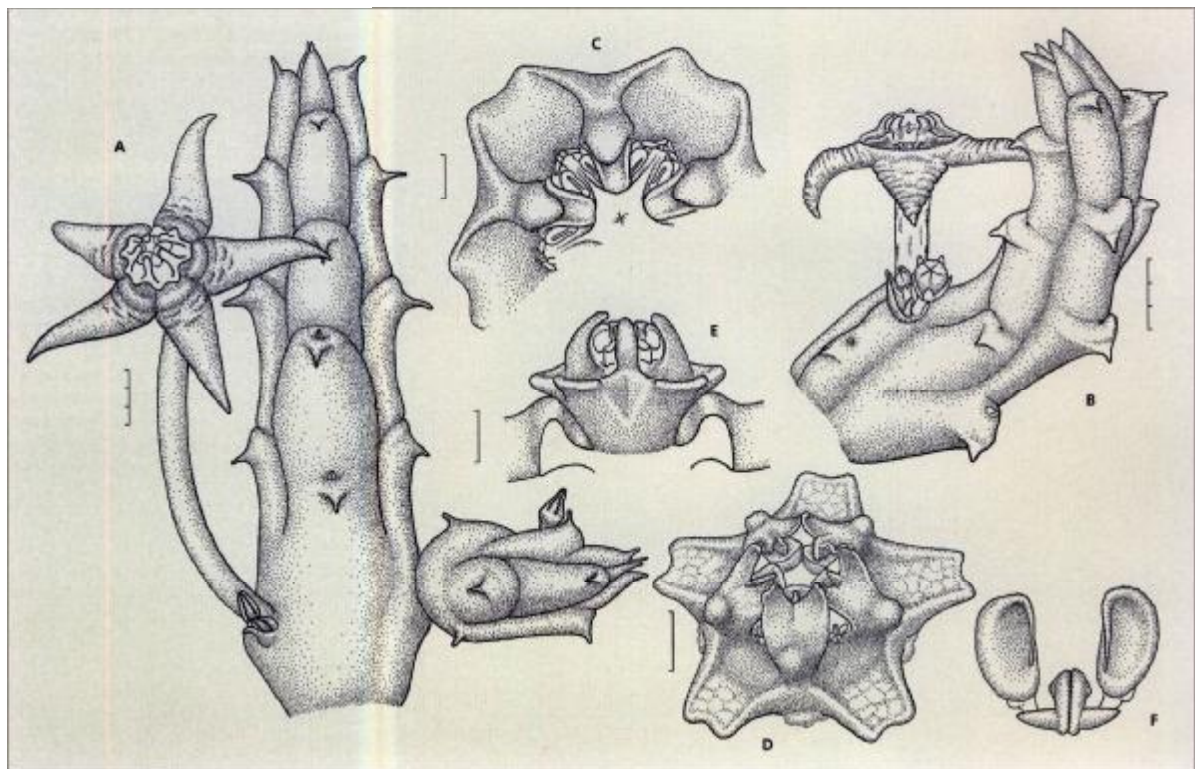


Fig. 10.29. *Orbea miscella*. A, B, stem bearing flowers. C, D, face view of gynostegium. E, side view of centre of dissected flower. F, pollinarium. Scale bars: A, 3 mm; B, 3 mm; C, 0.5 mm; D, 1 mm; E, 1 mm; F, 0.25 mm (at B). Drawn from: A, E, *PVB* 1578, north-west of Cradock; B, C, F, *PVB* 3237, Richmond; D, *PVB* 4250, north of Klipplaat.

ORBEA MISCELLA

broad, spreading to touch surface of corolla at mouth of tube, $\pm$ transversely rectangular with slight to deep deltate notch in apex; *inner lobes* 0.5-1.0 mm long, adpressed to backs of anthers but usually much shorter than them, slightly to strongly dorsiventrally flattened, $\pm$ deltoid and obtuse or rarely $\pm$ rectangular and broadening towards deeply emarginate apex, sometimes with small obtuse dorsal gibbosity near base, joined to outer series dorsally towards base.

Distribution and habitat

Orbea miscella is widely distributed in the Great Karoo, from Fraserburg north-eastwards to Richmond, Hanover and Cradock and south-eastwards to Willowmore and Steytlerville (Bruyns 1982c; 1986a).

Plants are quite extraordinarily inconspicuous and difficult to locate in habitat and the species is almost certainly more widely distributed and common than the records indicate. Most encounters with it involve a single specimen only.

Specimens are usually found in flattish areas on low stony ridges where they grow among stones and small karroid bushes usually not taller than 30 cm.

Diagnostic features and relationships

In *O. miscella* the stems are slender (mostly about 5 mm thick) and small (often not more than 20 mm tall) and form small clumps often only 50-80 mm across. In some cases several of these clumps are connected by runners beneath the ground which can spread for up to 150 mm before emerging again above the surface. The tiny stems are usually brownish in the field but become green in cultivation. They have small tubercles arranged into four angles along them and each tubercle is tipped with a



Fig. 10.30. *O. miscella*, PVB 8980, north of Klaarstroom, some stems removed from ground to show extensive underground growth.

minute tooth.

Flowers are produced on a short peduncle which develops near the base of the stem. They are held facing upwards on a pedicel of extremely variable length and are themselves also very variable in many features. Usually small (10-18 mm across) and purple-brown inside, the flowers are not pretty and often emit a very bad smell of excrement. The lobes vary from ovate to lanceolate, sometimes nearly flat but mostly convex with the margins well folded back. There is usually a thickened annulus around the corona which may be prominent and divided into five discrete 'islands' (one below each lobe) but may also be very insignificant. The annulus gives rise to a small corolla tube around the base of the gynostegium. In most cases the inner surface is

almost smooth with a few scattered rugosities but some flowers have been seen (fig. 10.34) where it is deeply reticulated-rugulose on the lobes.

The corona is usually raised on a slight stipe to protrude beyond the tube. It, too, is very variable in size and, for example, the gynostegium of the type is about half the diameter of that in subsequent collections from around Klipp-laar. The outer lobes are roughly rectangular (sometimes apically notched) and spread on the top of the annulus while the inner lobes are small and variously shaped and they may either equal or just exceed the anthers. There is often plenty of nectar secreted on the outer lobes.

The stems of this remarkable species bear some resemblance to those of *O. ubomboensis*, being similarly small and uniformly coloured



Fig. 10.31. *O. miscella*, PVB 8980, north of Klaarstroom. Plant in habitat in crevices on a small shale outcrop, December 2001.

ORBEA CAUDATA



Fig. 10.32. *O. miscella*, PVB 1578, north-west of Cradock. Plants in this area seem generally to have narrow and fairly smooth corolla lobes as here.



Fig. 10.33. *O. miscella*, PVB 4909, north of Willowmore. Very small flowers more or less continuous annulus.

with very small tubercles and no stipular denticles. In *O. miscella* the usually solitary inflorescence arises near the base of the stem while in *O. ubomboensis* several are produced on each stem near its apex. The flowers of the two are similar in size. However, although the stems and the flower of *O. miscella* are unusually small, there are several features which are typical of many species which Leach (1978) included in *Orbea*. These include the usually solitary, basal, few-flowered inflorescences, the rugulose inside of the corolla and the raised, annular thickening forming a small corolla tube. Several of these features are absent in *O. ubomboensis*. In addition, the respective coronas, while superficially similar, show many differences and that of *O. miscella*, while again small, is more like that found in *Orbea verrucosa*, for example. Molecular data place it in an unresolved polytomy together with a large 'Orbea-branch' so that its relationship to the remainder of *Orbea* remains unresolved.

History

The 'mixed up' *Stapelia* was described by N.E. Brown from material collected by Eustace Pillans near Klipplaat in the Eastern Cape and sent to Kew by N.S. Pillans. Brown was much puzzled by this species and felt that it was 'almost certainly of hybrid origin between a *Duvalia* and some other genus, possibly a *Caralluma*' (Brown 1907-09). Lückhoff saw some material of it (though it remains unclear which material this was, as none was cited) and transferred it to *Stultitia*, presumably because of the presence of an annulus. Leach wrote '*Orbea miscella* (N.E. Br.) Leach probably a hybrid with *O. verrucosa* one parent, L.C. Leach 1975' on the type at Kew and so also believed it to be a hybrid. This is in fact quite out of the question (Bruyns 1986a). Leach (1978a) was unsure what to do with it while Gilbert (1990) placed it in *Pachycymbium*.



Fig. 10.34. *O. miscella*, PVB 4250, north of Klipplaat. The corolla in plants from this locality has a particularly rough inner surface and the annulus is divided into five islands.

5. *Orbea caudata*

Orbea caudata (N.E. Br.) Bruyns, *Aloe* 37: 73 (2000).
Caralluma caudata N.E. Br., *Fl. Trop. Afr.* 4 (j): 485 (1903).

Orbeopsis caudata (N.E. Br.) L.C. Leach,
Excelsa Taxon. Ser. 1: 68 (1978).
Type: Malawi, Namadzi (Namas), Cameron 25 (K).

Small succulent forming dense to diffuse clump up to 500 mm diam., not at all rhizomatous. Stems 40-150 mm long, 6-11 mm thick (excluding teeth), slender, erect to decumbent, pale greenish grey to olive-green flecked (sometimes intensely) with red-purple; tubercles 6-25 mm long, arranged loosely into 4 obtuse rows along stem $\pm$ without groove between rows, tapering into slender conical attenuate spreading to ascending tooth, with 1-2 slight lateral swellings around middle but no denticles, part above swellings gradually withering away. Inflorescence usually only 1 per stem between middle and apex, of (2-) 3-7 extremely smelly flowers opening $\pm$ simultaneously from slight peduncular swelling, with slender bracts up to 5 mm long; pedicel 9-20 mm long, 1.5-2.0 mm thick, horizontal to ascending, pale pink; sepals 6-7 mm long, 1.5 mm broad at base, lanceolate, acuminate, apices sometimes slightly reflexed. Corolla 35-60 (-95) mm diam., rotate, very deeply lobed; outside smooth, pale cream-green dotted with purple-red; inside yellow to greenish dotted with purple-brown to maroon to brick-red becoming fainter and finer towards tips of lobes and coalescing towards centre, lightly rugulose becoming more coarse around middle of lobes (nearly smooth towards tips and in tube), covered with fine papillae and with coarser clavate to acute papillae in tube; tube 1.5-2.0 mm deep, shallowly bowl-shaped, pentagonal, just containing lower half of gynostegium, with slight thickening of corolla towards mouth; lobes 18-25 (-35) mm long, 5-7 (-11) mm broad at base, spreading, with ovate base tapering gradually to slender acute tip, convex from reflexed margins, with scattered slender spatulate purple cilia 1-4 mm long along most of margin except near tips. Corona 3-4 mm tall, 6-8 mm broad, raised above base of tube on stout obtusely pentagonal deep purple-red stipe; outer lobes 1.5-2.0 mm long, subquadrate, slightly bifid into small obtuse to deltoid diverging lobules, ascending, usually held slightly above corolla, purple-red except for broad cream patches on lobules; inner lobes 1.0-1.5 mm long, 0.7-1.0 mm broad, adpressed to backs of anthers and usually exceeding them to meet and overlap in centre, dorsiventrally flattened, linear and often somewhat rectangular, obtuse, slightly gibbous on rear which is fused laterally to outer lobes, rear and margins and tips purple-red, upper surface cream to white.

Orbea caudata is an exclusively tropical species found in north-eastern Namibia, probably in the adjacent parts of Angola, northern Botswana, Zimbabwe and sporadically further north in Tanzania, Zambia, Malawi and Moçambique.

This species can easily be distinguished from all other members of Leach's former genus *Orbeopsis* by the slender stems with long and narrow tubercles (which are only approached in *O. gerstneri* subsp. *gerstneri*) and by the relatively few-flowered inflores-



Fig. 10.35. *O. caudata* subsp. *caudata*, PVB 7756, Njuli Quarry, Malawi.

cences. Another reliable but less easily seen difference lies in the short, almost rectangular inner corona lobes which are flattened on the backs of the anthers. Unlike the position in all the others, they do not possess any dorsal horns and do not rise up in the centre at all.

5a. *Orbea caudata* subsp. *caudata*

Caralluma caudata var. *fusca* C.A.Lückh. in A.C. White & B. Sloane, Stap., ed. 2, 3:144 (1937).
Lectotype: White & Sloane, Stap., ed. 2, 1: fig. 287.

Caralluma praegracilis Oberm. in A.C. White & B. Sloane, Stap., ed. 2, 3:161 (1937).

Type: South Africa, Natal, Nongoma, Gerstner 752 (missing).

Lectotype: White & Sloane, Stap., ed. 2, 3: fig. 1212.

Stems olive-green strongly flecked with purplish; tubercles 5-10 (-15) mm long.

Distribution and habitat

Orbea caudata subsp. *caudata* occurs further north-east than the other subspecies and in somewhat wetter areas. It is known from Tanzania, Zambia, Malawi and Moçambique and is apparently only common around Mbala in Zambia (Leach 1973), being otherwise fairly rare. It is locally extremely common near Blantyre in Malawi, but seems to be known in this area from only a single locality. In Mocambique it is known from a single collection made near Mandimba by A. Rocha da Torre. The

record from Nongoma, Zululand, of F.J. Gerstner (the type of *Caralluma praegracilis*) is almost certainly an error as it has never been found so far south again.

Subsp. *caudata* grows on gently sloping granite domes, sometimes together with Aloes and other succulents. Plants near Blantyre grow among small grasses and clumps of *Opuntia* in patches of soil on a very disturbed, low, granitic dome.

Diagnostic features and relationships

Specimens of subsp. *caudata* form large and somewhat untidy clumps up to 0.5 m in diameter. They are not at all rhizomatous.

The flowers are produced in relatively small clusters (often only three or four flowers together in a group) at quite variable heights on the stem and often towards the tips. They make up for their low numbers by being brightly coloured and emitting a particularly strong, bad smell, accurately described as 'of something dead'. Apart from this rather repellent feature, they are actually very pretty: usually they have a yellow to greenish background on which there are numerous small, usually round, purple-brown to maroon spots. These spots coalesce towards the centre. Wholly brown to brick-red or maroon flowers sometimes occur.

The corona is relatively low and flat and much simpler than that in the other species of '*Orbeopsis*'. The outer lobes spread outwards and are more or less truncate. The inner lobes are adpressed to the anthers and hide them from view but they do not rise in a column in the centre. They have a small transverse dorsal ridge near the base. The ends of the outer lobes and much of the visible part of the inner lobes are usually white while the rest of the lobes are red. They are somewhat shiny with secreted nectar.

History

Subsp. *caudata* was first sent to Kew in about 1894 by Kenneth J. Cameron, a planter in Malawi for the African Lakes Corporation (Reynolds 1966). His collection was made near Namadzi, between Zomba and Blantyre in southern Malawi. Very few records of it seem to have been made (Leach 1973), though it was, at one time, widely distributed in cultivation. Material was first found in Moçambique sometime before but it has never been collected there again.

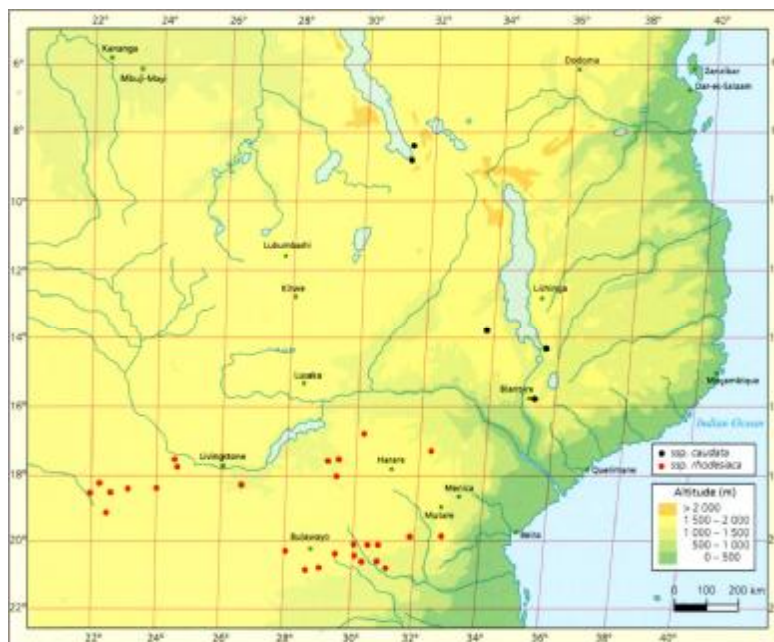


Fig. 10.36. Distribution of *Orbea caudata*.

Key to the subspecies of *O. caudata*

Stems olive-green with purplish flecks, tubercles 5-10 mm long	5a. subsp. <i>caudata</i>
Stems grey-green with purplish flecks, tubercles 12-25 mm long	5b. subsp. <i>rhodesiaca</i>

ORBEA CAUDATA



Fig. 10.37. *O. caudata* subsp. *caudata*, PVB 7756, Njuli Quarry, Malawi, a large specimen over half a meter in diameter growing in shallow soils with short grasses on a low granite dome, January 1999.



Fig. 10.38. *O. caudata* subsp. *caudata*, PVB 7756, Njuli Quarry, Malawi, in habitat, January 1999.

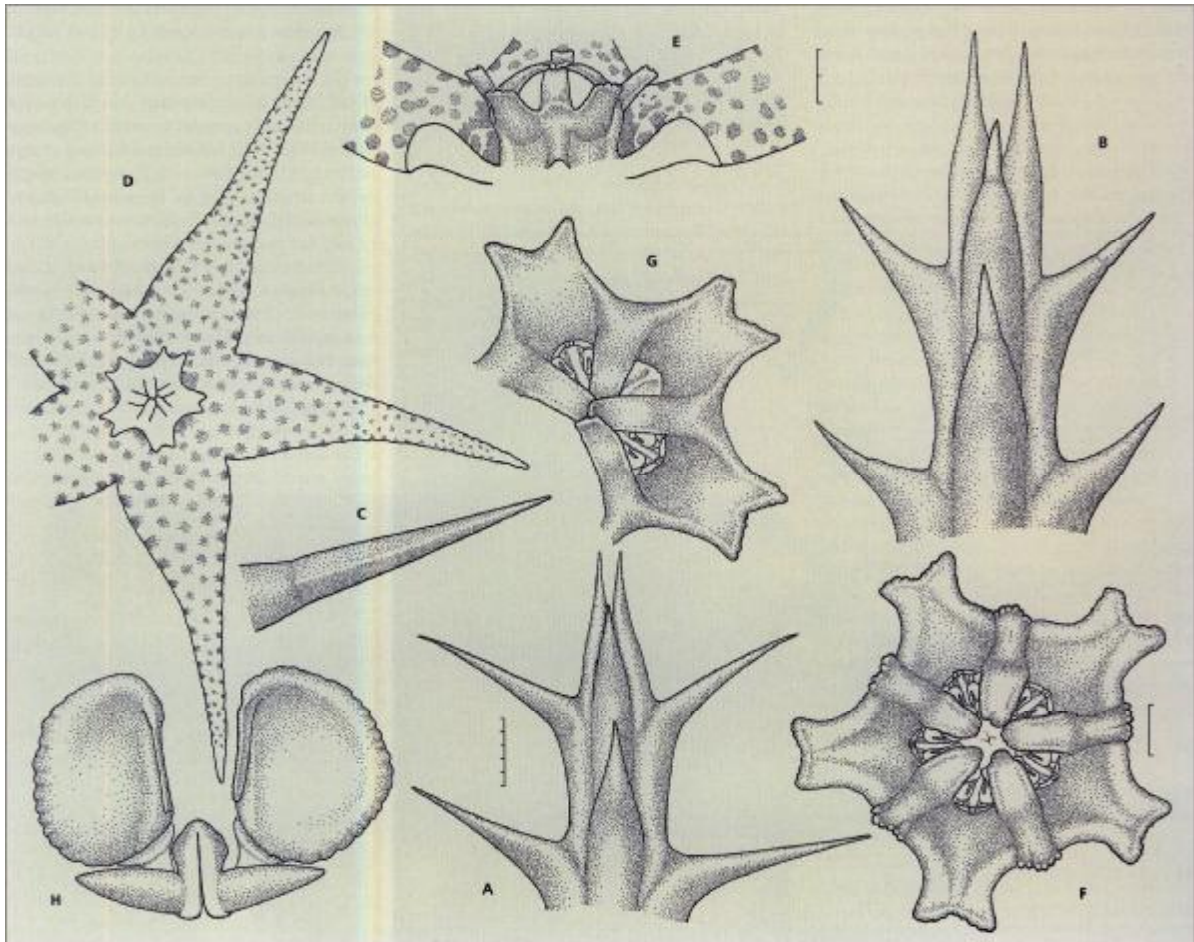


Fig. 10.39. *Orbea caudata* (B, C, subsp. *caudata*; A, D, E, F, G, H, subsp. *rhodesiaca*). A, B, apex of stem. C, apex of tubercle. D, face view of (most of) flower. E, side view of centre of dissected flower. F, G, face view of gynostegium (or part of it). H, pollinarium. Scale bars: A, B, D, 5 mm (at A); C, 2 mm (at A); E, 2 mm; F, G, 1 mm (at F); H, 0.25 mm (at A). Drawn from: B, C, PVB 7756, Njuli Quarry, Malawi; A, E, PVB 6941, Seronga, Okavango, Botswana; D, G, PVB 6499, Etsha 6, Okavango, Botswana; F, H, PVB 2292, Lake Liambesi, Namibia.

5b. *Orbea caudata* subsp. *rhodesiaca*

Orbea caudata subsp. *rhodesiaca* (L.C. Leach)

Bruyns, *Aloe* 37: 73 (2001).

Caralluma caudata subsp. *rhodesiaca* L.C. Leach,
Bothalia 11: 134 (1973).

Orbeopsis caudata subsp. *rhodesiaca* (L.C. Leach)

L.C. Leach, *Excelsa Taxon. Ser.* 1: 68 (1978).

Type: Zimbabwe, Mberengwa distr., south of
Mnene Mission, Leach & Bullock 13145 (ZSS,
holo.: BM, BOL, BR, K, LISC, PRE, SRGH, iso.).

Caralluma chibensis C.A. Lückh., *S. African Gard.*
& *Country Life* 25: 56 (1935).

Caralluma caudata var. *chibensis* (C.A. Lückh.)

C.A. Lückh. in A.C. White & B. Sloane, *Stap.*,
ed. 2, 1: 352 (1937).

Type: Zimbabwe, Chibbi, 1931, Jackson sub Lückhoff
182 (missing).

Lectotype: *S. African Gard. & Country Life* 25:
upper left hand photograph, p. 56.

Caralluma caudata var. *milleri* Nel in A.C. White &
B. Sloane, *Stap.*, ed. 2, 3: 1158 (1937).

Type: Angola, Okavango River, Miller sub STE 7390 (missing).

Lectotype: White & Sloane, *Stap.*, ed. 2, 3: fig. 1211.

Caralluma caudata var. *stevensonii* Oberm. in A.C.

White & B. Sloane, *Stap.*, ed. 2, 3: 1156 (1937).

Type: Zimbabwe, near Harare, Stevenson sub
Transvaal Mus. 34947 (missing).

Stems grey-green finely flecked with red-purple; tubercles
12–25 mm long.

Distribution and habitat

Subsp. *rhodesiaca* is found in the extreme north-east of Namibia in the Caprivi Strip, probably also in the adjacent parts of Angola (although there are no specimens from this area) and it is widespread in the northern parts of Botswana and over most of Zimbabwe except for the arid south near the Limpopo. It is, as Leach (1973) said, probably the most common stapeliad in Zimbabwe and it is also very plentiful in the sandy regions north of the Okavango Delta of Botswana.

Subsp. *rhodesiaca* is usually found on the floor of relatively open forest, frequently in *Colophospermum mopane* or *Brachystegia* woodland. Specimens are rarely found on granite domes, where they have been seen a few times in southern Zimbabwe among small clumps of the resurrection bush, *Myrothamnus flabellifolius*.

Diagnostic features and relationships

Plants of subsp. *rhodesiaca* form a fairly dense and usually small clump, in the open or around the base of a tree. Like the typical subspecies, they are not at all rhizomatous. Where growing in open areas, their long, slender tubercles



Fig. 10.40. *O. caudata* subsp. *rhodesiaca*, PVB 6941, Seronga, Okavango, Botswana.



Fig. 10.41. *O. caudata* subsp. *rhodesiaca*, PVB 6499, Etsha 6, Okavango, Botswana.

and grey-green colour mottled with purple can make the plants surprisingly inconspicuous, especially if they are growing among tufts of grass.

In subsp. *rhodesiaca* the stems have longer, more slender tubercles than in subsp. *caudata*. These tubercles are usually about 15 mm long and taper into a fine, soft point. In this respect and in their colour they closely resemble the stems of *Orbea umbracula*, from which the plants of *O. caudata* are, in fact, difficult to separate.

Flowers are usually produced in small clusters of four or five and usually at most two or three flowers in a cluster are open at any one time. The flower is more or less flat with slender lobes spreading widely with quite long, spatulate cilia along their margins. There is a small, strongly pentagonal tube in the centre. The flowers are almost always bright yellow with fine, circular, maroon spots. Occasionally darker flowers are found but they are rarer than in subsp. *caudata*. Towards the centre there is a pentagonal, slightly darker area which begins just outside the tube. This change in colouring is caused partly by the spots becoming closer

together and even coalescing towards the base of the tube but mainly by small papillae whose apical cell is particularly broadly swollen into an unusual mammosc shape and is dark purple-black. These papillae become denser lower down in the tube. The flowers emit a strong excrement-like odour.

History

Subsp. *rhodesiaca* was well known at the time of the appearance of White & Sloane (1937), having been found in Zimbabwe by Miss Jackson and the civil engineer R.H.R. Stevenson before then, though the earliest record that I have seen was made by Frederick Eyles in February 1936. A.H. Miller seems to have been the first to find it along the Okavango River, apparently in southern Angola (Leach 1973), and it has subsequently been found in Namibia and Botswana, mainly to the east of this river.



Fig. 10.42. *O. caudata* subsp. *rhodesiaca*, PVB 7449, north of Gokwe, Zimbabwe.

ORBEA MELANANTHA

6. *Orbea melanantha*

- Orbea melanantha* (Schltr.) Bruyns, *Aloe* 37: 76 (2001).
Stapelia melanantha Schltr., *Bot. Jahrb. Syst.* 38: 50 (1905).
Caralluma melanantha (Schltr.) N.E. Br. Fl. Cap. 4 (1): 885 (1909).
Orbeopsis melanantha (Schltr.) L.C. Leach, *Excelsa Taxon. Ser.* 1:66 (1978).
 Type: South Africa, Transvaal, stony flats near Sandloop, *Schlechter* 4694 (missing).
 Neotype: South Africa, Transvaal, Bantolierkop, Leach 9757 (K, holo.; KIEL, LMAI, PREI, SRGHI, iso.).
Caralluma leendertziae N.E. Br., *Ann. Transvaal Mus.* 2: 47 (1909).
 Type: Transvaal, Potgietersrust, *Leendertz* 1279 (K).
Stapelia furcata N.E. Br. Fl. Cap. 4 (1): 973 (1909).
 Type: Transvaal, Todd (K).
Caralluma rubiginosa Werdermann, *Feddes Repert. Spec. Nov. Regni Veg.* 30: 54 (1932).
 Type: cult. Berlin-Dahlem (missing).
Caralluma melanantha var. *sousae* A. White ex Gomes e Sousa, *Moçambique Doc. Trim.* 4: 46 (1935).
 Type: Moçambique, Maputo distr., Mangulane, Gomes e Sousa (missing).
Caralluma australis Nel in A.C. White & B. Sloane, *Stap.*, ed. 2, 3:153 (1937).
 Type: Transvaal, Pietersburg distr., *Kirsten* sub STE 5881 (NBG).

Succulent forming mat to 1 m diam., not rhizomatous. Stems 30-100 mm long, (10-) 15-40 mm thick (excluding teeth), usually very stout, decumbent, pale green speckled with red-brown; *tubercles* 6-15 mm long, joined into 4 continuous obtuse wing-like angles along stems with deep groove between angles, laterally flattened, tapering into stout deltoid acute tooth with small denticle on either side near tip, tip gradually becoming hardened and covered with yellowish corky layer. *Inflorescence* 1 (-2)

per stem near or above middle, of 3-13 simultaneously opening flowers from stout peduncle up to 15 mm long and 6-10 mm thick, with lanceolate to ovate laterally toothed subulate bracts 4-8 mm long; *pedicel* 15-45 mm long, 3-4 mm thick, ascending to spreading; *sepals* 6-10 mm long, 2-3 mm broad at base, ovate-lanceolate, acuminate. *Corolla* 40-65 mm diam., rotate; outside smooth, pale cream suffused with brown; inside deep red-brown to maroon- or purple-black sometimes finely spotted with yellow, finely rugulose on lobes becoming deeply ± concentrically rugulose in tube, surface finely papillate all over with occasional larger spike-like papillae up to 1 mm long; *tube* 2.5-4.0 mm deep, short, cupular, containing ± whole of gynostegium, with corolla much thickened at mouth; *lobes* 14-18 mm long, 9-14 mm broad at base, broadly deltate-ovate, acute, spreading with tips often reflexed, with vibratile clavate purple cilia 2-5 mm long along margins. *Corona* ± 3 mm tall, 8-9 mm broad, raised above base of tube by stout pentagonal stipe < 1 mm long, red-brown to purple-black; *outer lobes* 3-4 mm long, 3 mm broad, ascending-spreading, flat, ± square (often widening towards apex) with 2 or more often spreading short apical teeth, above with 2-3 radial raised tuberculate ridges; *inner lobes* 2-3 mm long, adpressed to backs of anthers for ± half anthers' length then ascending and nearly equalling them, dorsiventrally flattened near base with raised crenulate margins (so concave there) becoming laterally flattened above, with erect to slightly recurved dorsal horn just behind somewhat obtuse ± horizontal apex (apex sometimes absent below dorsal horn) and second dorsal horn occasionally present, with dorsal tuberculate ridges and horns confluent with outer series towards base.

Distribution and habitat

Orbea melanantha has a rather more restricted distribution than its close relative *O. lutea*. It has been recorded in Moçambique from near sea level around Maputo to 300 m above sea level near Moamba, with a single record from further north near Vilankulo (no specimen), also close to the coast (Gomes e Sousa & Esteves de Sousa 1947). It is mainly known at relatively high altitudes of between 1 000 and 1700 m

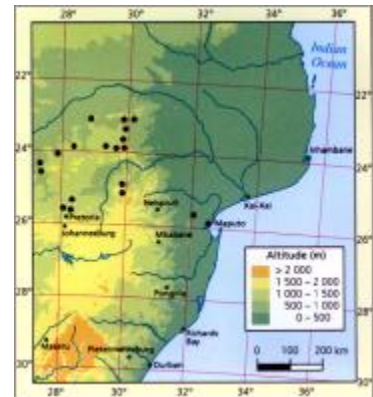


Fig. 10.43. Distribution of *Orbea melanantha*.

in the northern part of South Africa where it is found from the Soutpansberg south-wards and westwards to near Pretoria and towards the edge of the escarpment near Tzaneen and around Groblersdal. It is often locally very common and although it occurs near to where *O. lutea* has been recorded, the two species have never been observed growing sympatrically.

Specimens of *O. melanantha* are usually found among *Acacia* trees on stony ground with short grasses and some succulents and they also occur occasionally on shallow soil on granite domes. Those in Moçambique have sometimes been recorded as growing in sand on the floor of open *Brachystegia* forest (Gomes e Sousa & Esteves de Sousa 1947).

Diagnostic features and relationships

Plants of *O. melanantha* form mats up to 1 m across spreading entirely on the surface of the soil and with no trace of underground

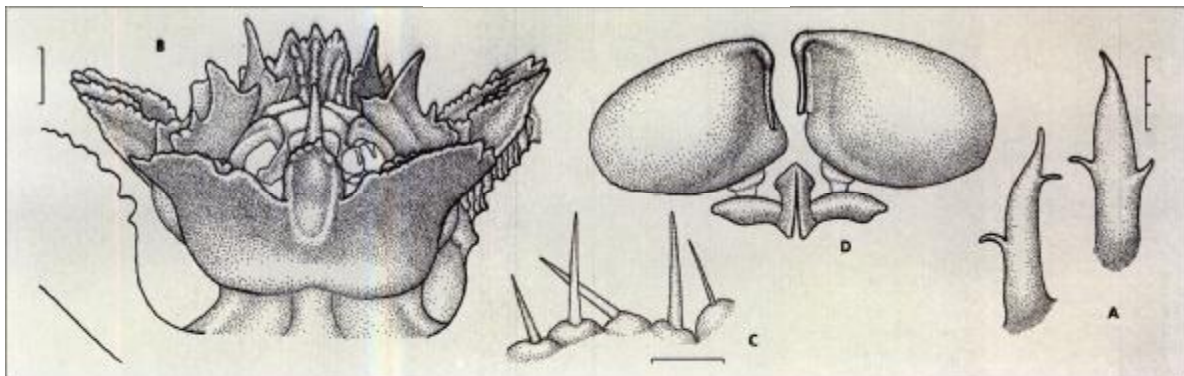


Fig. 10.44. *Orbea melanantha*. A, bracts from inflorescence. B, side view of centre of dissected flower. C, papillae inside corolla. D, pollinarium. Scale bars: A, 3 mm; B, 1 mm; C, 1 mm; D, 0.25 mm (at C). Drawn from: PVB 6536, 10 km north of Thabazimbi.

rhizomes. The stems are relatively short and proportionally very stout, up to 40 mm thick and often not much more than two to three times as tall as broad. This usually makes them considerably stouter and squatter than those of *O. lutea*, where they occur near one another. They are pale green mottled with red-brown and have prominent deltoid tubercles which are joined into thick wings along the stem.

Flowers are borne on a thick peduncle arising usually around the middle of the stem. While they are not produced in such large numbers as in some other members of the former genus *Orbeopsis*, they are still very striking, both visually and olfactorily. On the inside they have a deep reddish to nearly black colour which may be lightly spotted with yellow and they emit a frightful smell of excrement. Like *O. gerstneri* they are short-lived and remain open usually for only one or two days. The corolla is between 40 and 65 mm across and is almost completely flat when fully open, with relatively short deltate lobes which spread out

fully. The inside is densely rugulose with fine, spike-like papillae on the ridges which, in some cases, cause the corolla to appear quite furry. There are quite long spatulate cilia along the margins of the lobes.

In the centre of the flower, sunken into a slight tube so as to be more or less flush with the surface, is the gynostegium, which is similarly coloured to the rest of the inside. The outer lobes are broad, filling completely the area between the inner lobes, and they are usually heavily radially ridged on their upper surface. The inner lobes almost equal the anthers and usually have a somewhat recurved horn near the apex, with additional ridges and tubercles dorsally near the base.

Orbea melanantha and *O. lutea* are not easily confused in the region where they occur near one another. The former has very dark flowers with short, broad lobes and the latter has larger, bright yellow flowers with much longer and narrower lobes. However, *O. lutea* is so variable that, when it is considered

over its whole distribution, distinguishing the two species proves to be more difficult. Their respective outer coronas are very similar and it is mainly on the inner lobes that they can be separated most reliably. In both *O. lutea* and *O. melanantha* each inner corona lobe consists of a thickened part addressed to the back of the anther and usually slightly shorter than it. In *O. lutea* there are two laterally flattened dorsal horns behind this, one longer one near the apex and a much shorter one behind this but still somewhat above the base. The lobe itself is often barely separable from the larger dorsal horn and is usually visible only as a slight swelling or protuberance at its base.

In *O. melanantha* the lobe itself is again shorter than the anther. Behind its apex is a recurved, usually somewhat cylindrical horn rarely with another small one slightly behind this. Much lower down dorsally and more or less in series with the outer lobes, the lobe is excavated or furrowed with an irregularly toothed, transverse ridge. This is completely lacking in *O. lutea*.

History

Orbea melanantha was discovered in April 1894 in the former Transvaal near Pietersburg by Rudolf Schlechter and he named it *Stapelia melanantha* himself. In 1909 N.E. Brown transferred it to *Caralluma*. In the same volume he described flowers of another collection as *Stapelia furcata* and elsewhere he named yet a further collection as *Caralluma leendertziae*, both of which were realised by White & Sloane (1937) to be the same as Schlechter's species. Leach (1970b) found several more synonyms.



Fig. 10.45. *O. melanantha*, PVB 6592, near Soekmekaar, in habitat, January 1996.



Fig. 10.46. *O. melanantha*, PVB 7799, near Bulge River, Waterberg.



Fig. 10.47. *O. melanantha*, PVB 6592, near Soekmekaar. Plants form large mats on low granite domes at this locality. The lens-cap gives some idea of the diameter of the plant, in habitat, January 1996.

ORBEA ALBOCASTANEA

7. *Orbea albocastanea*

Orbea albocastanea (Marloth) Bruyns, *Aloe* 37: 73 (2001).

Stapelia albocastanea Marloth, *Trans. Roy. Soc. South Africa* 3:24 (1913).

Caralluma albocastanea (Marloth) L.C. Leach, *J. S. African Bot.* 36: 174 (1970).

Orbeopsis albocastanea (Marloth) L.C. Leach, *Excelsa Taxon. Ser.* 1: 65 (1978).

Type: Namibia, Maltahöhe, Marloth 5110 (PRE).

Stapelia caroli-schmidtii Dinter & A. Berger, *Bot. Jahrb. Syst.* 50, Suppl.: 592 (1914).

Type: Namibia, flats near Bullsport, Dinter 2105 (SAM).

Small succulent forming mat to 0.5 (-1.0) m diam., sometimes rhizomatous. Stems 20-80 mm long, 10-16 mm thick (excluding teeth), stout, decumbent, sometimes rhizomatous, often uniformly pale green but sometimes mottled with purple-red; tubercles 2-5 (-9) mm long, joined roughly into 4 very broadly obtuse angles along stem with slight groove between angles, laterally flattened, tapering into short conical deltoid acute tooth sometimes with pair of small stipular denticles near apex. Inflorescence 1 (-2) per stem near base, of 3-30 flowers opening in succession from short stout truncate often branched peduncle (often at least 10 mm long and 3-4 mm thick) near base of stem; pedicel (15-) 30-60 mm long, 1.5-2.0 mm thick, ascending to spreading on ground and holding flower facing at least partly upward; sepals 2.5-3.0 mm long, 1.5 mm broad at base, ovate,

acuminate. Corolla 18-30 mm diam., rotate, deeply lobed; outside smooth pale green with a few small red-brown dots; inside irregularly rugulose-papillate, white to cream, irregularly dotted with purple-brown with dots becoming finer around corona; tube $\pm$ 1.5 mm long, 4-7 mm broad, shallowly cupular, containing base of gynostegium, with corolla distinctly thickened around mouth; lobes 6-12 mm long, 4-5 mm broad at base, ovate-deltate, acute, spreading, convex from reflexed margins, with scattered spatulate cilia up to 2.5 mm long along margins. Corona $\pm$ 6 mm tall, 8 mm broad, raised only very slightly above base of tube on very short stipe; outer lobes 2.0-2.5 mm long, 1.5-2.0 mm broad, ascending-spreading, $\pm$ rectangular with deeply notched apex, upper surface with 2 or more raised radial tuberculate ridges (usually darker brown between them and cream or pinkish outside them); inner lobes 4-5 mm long, adpressed to backs of anthers for half anthers' length then erect and somewhat recurved above, laterally flattened, linear, narrowing slightly to obtuse apex, with spreading-recurved terete dorsal horn near base $\pm$ 2 mm long, fused laterally at base to outer series, cream to brown.

Distribution and habitat

Orbea albocastanea occurs in Namibia in two apparently disjunct areas. One of these lies to the west and north-west of Maltahöhe, where the species is found from the south-eastern foot of the Naukluft to west of Maltahöhe. The other is situated roughly 300 km to the south-east of this, around the base of and in the Great Karas Mountains, south-east of Keetmanshoop.

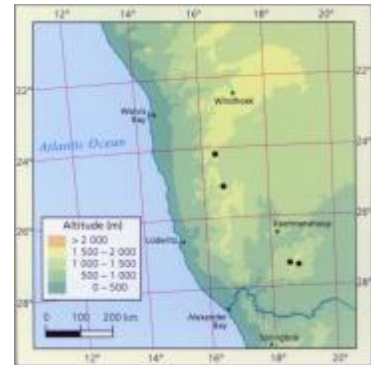


Fig. 1048. Distribution of *Orbea albocastanea*.

Recent collections have revealed it both on the western and eastern sides of the Great Karas Mountains.

In the Great Karas Mountains it has been seen several times from the foothills of the mountains at 1 200-1 300 m up to some of the higher plateaux at altitudes of 1 600-1 700 m. It generally grows on stony ground on soils derived from sandstones or granite, under small bushes and can become locally quite common. Specimens from west of Maltahöhe grew in a flat, pan-like area under very short bushes on calcrete.

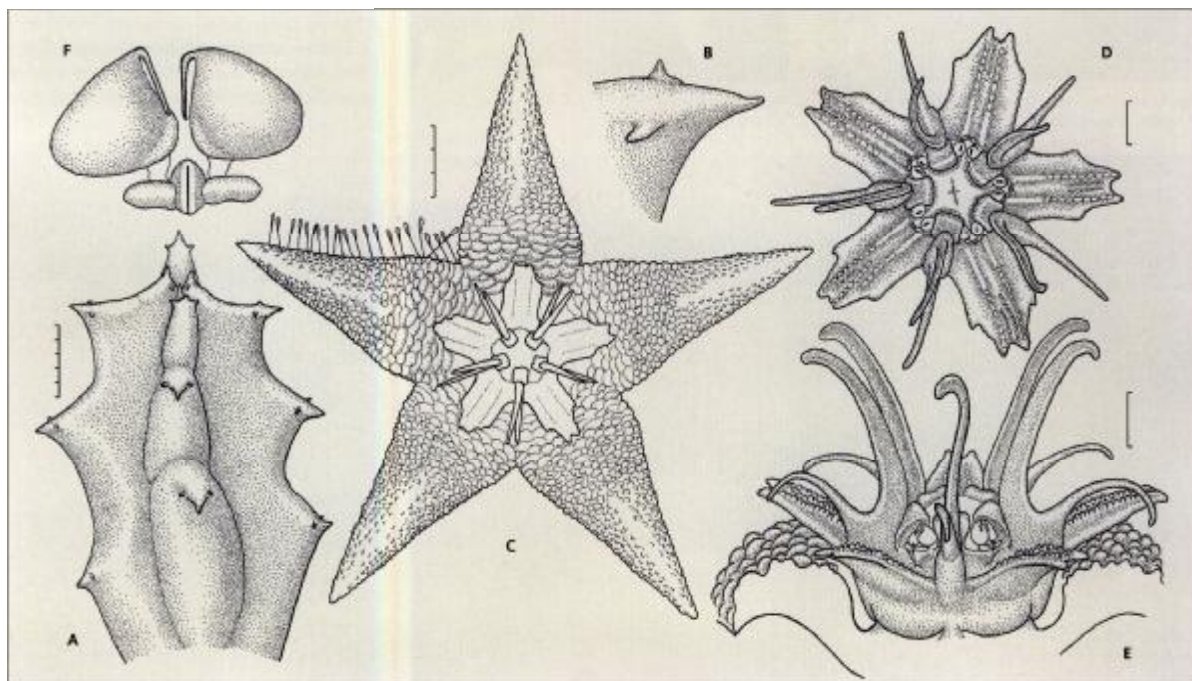


Fig. 1049. *Orbea albocastanea*. A, apex of stem. B, apex of tubercle. C, face view of flower. D, face view of gynostegium. E, side view of centre of dissected flower. F, pollinarium. Scale bars: A, 5 mm; B, 1 mm (at C); C, 3 mm; D, 1 mm; E, 1 mm; F, 0.25 mm (at C). Drawn from: PVB 3543, eastern side of the Great Karas Mountains, Namibia.

Diagnostic features and relationships

Clumps of *O. albocastanea* can become quite large, up to 0.5 m in diameter and even larger on occasion. The stems are usually very short (sometimes only 20 mm long) but are quite stout and become densely packed into mats. With their short stems and mat-forming habit, the plants may bear some resemblance to specimens of *Piранthus* with which, in the Great Karas Mountains, they have occasionally been found to grow. As in *O. knobelii*, there are also often subterranean runners which may be up to 150 mm long and these seem to develop particularly in cultivated plants and only rarely in the wild. The stems in both species are also a similar pale green sometimes mottled with purple-red.

Flowers are produced in dense bunches on a spreading and often slightly branched peduncle. The pedicels are long and spreading and often become entangled on the ground. On one peduncle there will usually be several flowers open and others at all stages of development.

As Dinter (1914) remarked, the colour of the flowers here is a great rarity amongst the stapeliads. This unusual colour is shared with *O. knobelii* and *O. ciliata*, but it is only to the first of these that *O. albocastanea* is closely allied. In both *O. albocastanea* and *O. knobelii* the flowers are white to cream, irregularly dotted with purple-brown, with an irregularly and transversely papillate-rugulose surface. At 18–30 mm across in *O. albocastanea*, the flowers are somewhat smaller than in *O. knobelii* and they have narrower lobes with the margins well folded back so that the upper surface is distinctly convex. There is a slight tube in the centre around the base of the gynostegium which is caused by the corolla becoming slightly thickened here.

The respective coronas are very similar. The outer lobes are narrower and often longer in *O. albocastanea* than in *O. knobelii* (the illustration in Leach (1970b), where they are shorter than in *O. knobelii*, was drawn from pressed material and so does not reflect the real position) and they have a dark, medial radial patch with two paler, often cream areas towards the margins. The inner lobes are usually also longer and more diverging than in *O. knobelii* and each has a considerably longer dorsal horn. The main differences between the two lie, therefore, in the longer peduncle and pedicels, the convex, more lanceolate corolla lobes in *O. albocastanea* and the shorter dorsal horns on the inner corona lobes in *O. knobelii*.

History

Orbea albocastanea was discovered by M. Kurt Dinter in the flats around Büllsport at the eastern foot of the Naukluft on 4. 4. 1911 and collected again by him near Kanus, south of the

Great Karas Mountains, in April 1913. Dinter and Berger named Dinter's collection from the eastern foot of the Naukluft as *Stapelia carolischmidtii* in honour of Karl Schmidt, one of the owners of the nursery business of Haage & Schmidt in Erfurt, Germany. This was published in a special supplement to the *Botanische Jahrbücher* that was issued to celebrate the 70th birthday of Adolf Engler. Here it appeared among a small selection of 'new' succulents discovered by Dinter in Namibia but this publication came out slightly after Marloth's account of *Stapelia albocastanea*. Marloth collected this somewhere near Maltahöhe around the beginning of 1912, for it flowered in his garden in Cape Town in February or March 1912. It was also collected by Pearson in January 1913 at the eastern foot of the Great Karas Mountains during the Percy Sladen Memorial Expedition to these mountains. It was therefore discovered and collected several times over a short period. Not much more is known of it today and it has not been recollected around the base of the Naukluft, although it is known a bit further south, near Maltahöhe.



Fig. 10.50. *O. albocastanea*, PVB 5771, western flank of Great Karas Mountains, Namibia.



Fig. 10.51. *O. albocastanea*, PVB 5667, south-west of Maltahöhe, Namibia.



Fig. 10.52. *O. albocastanea*, PVB 3543, eastern side of the Great Karas Mountains, Namibia, showing the dense somewhat branched inflorescence with flowers at all stages of development.



Fig. 10.53. *O. albocastanea*, PVB 3543, eastern side of the Great Karas Mountains, Namibia.

ORBEA KNOBELII

8. *Orbea knobelii*

Orbea knobelii (E.Phillips) Bruyns, *Aloe* 37: 75 (200).

Stapelia knobelii E.Phillips, *Fl. Pl. South Africa* 10: t. 363 (1930).

Caralluma knobelii (E.Phillips) E.Phillips, *Fl. Pl. South Africa* 15: t. 593 (1935).

Orbegopsis knobelii (E.Phillips) L.C.Leach, *Excelsa Taxon. Ser.* 1:65(1978).

Type: Botswana, near Molepolole, *Knobel sub PRE* 8308 (PRE).

Caralluma langii A.C.White & B.Sloane, *Stap.*, ed. 1: 61 (1933).

Caralluma knobelii var. *langii* (A.C.White & B.Sloane) A.C.White & B.Sloane, *Stap.*, ed. 2: 368 (1937).

Type: Botswana, near Gaborone, *Van Son sub White & Sloane* 113 (missing).

Lectotype: White & Sloane, *Stap.*, ed. 1: fig. 40.

Caralluma kalaharica Nel in A.C. White & B. Sloane, *Stap.*, ed. 2: 31165(1937).

Type: Botswana, north-west of Lake Ngami, Tsau, Nel (missing).

Lectotype: White & Sloane, *Stap.*, ed. 2: 3: fig. 1216.

Succulent forming clump to 0.5 m diam, often rhizomatous. *Stems* 30-100 mm long, 10-25 mm thick (excluding teeth), stout, decumbent and often subterranean for some distance then erect above ground, often uniformly grey-green but sometimes mottled with red-brown; *tubercles* 3-6 mm long, joined into 4 very broadly obtuse angles along stem with slight groove between angles, basally almost cylindrical then tapering into conical to laterally flattened deltoid acute often ascending tooth, sometimes with stipular denticles. *Inflorescence* 1 per stem in lower half, of 3-10 flowers opening in rapid succession from short peduncle (< 10 mm long); *pedicel* 10-15 mm long, 2.5-3.0 mm thick, ascending to spreading and holding flowers facing $\pm$ horizontally; *sepals* 3-5 mm long, 1.5-2.0 mm broad at base, ovate-lanceolate, acuminate. *Corolla* 25-35 mm diam., rotate; outside smooth, pale green; inside irregularly rugulose-papillate, white to cream (greenish), irregularly blotched with purple-brown; *tube* 1.5-2.0 mm long, 6-10 mm broad, shallowly cupular, containing base of gynostegium, with corolla distinctly thickened around mouth; *lobes* 10-14 mm long, 7-10 mm broad at base, ovate, acute, often somewhat reflexed, slightly convex above from reflexed margins, with scattered clavate-spathulate cilia up to 3 mm long along margin. *Corona* $\pm$ 5-6 mm tall, 7 mm broad, raised only ery slightly above base of tube on very short pentagonal stipe; *outer lobes* 1.5-3.0 mm long, 2 mm broad, ascend-

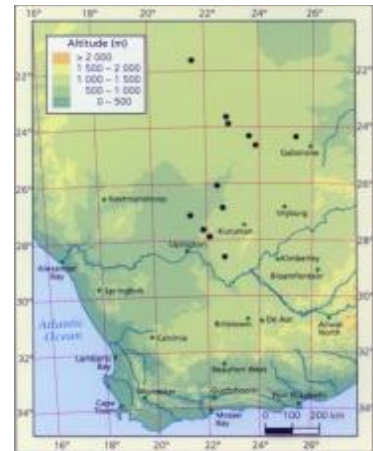


Fig. 10.54. Distribution of *Orbea knobelii*.

ing-spreading, $\pm$ square with notched-truncate apex, upper surface with at least 2 raised radial ridges (area between them usually dark purple-brown, outside them paler brown to cream); *inner lobes* 3.5-4.0 mm long, adpressed to

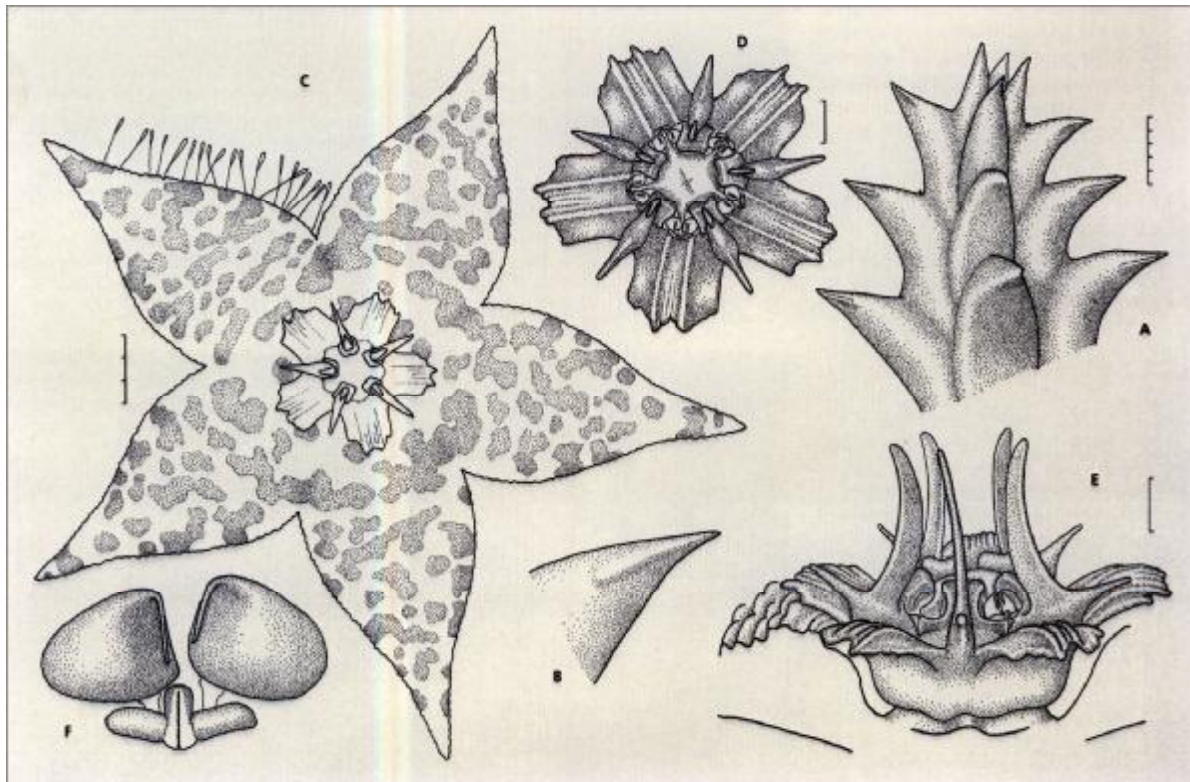


Fig. 10.55. *Orbea knobelii*. A, apex of stem. B, apex of tubercle. C, face view of flower. D, face view of gynostegium. E, side view of centre of dissected flower. F, pollinarium. Scale bars: A, 5 mm; B, 1 mm (at C); C, 3 mm; D, 1 mm; E, 1 mm; F, 0.25 mm (at C). Drawn from: PVB 3472, north of Upington.

backs of anthers for half anthers' length then erect, laterally flattened but becoming broader towards base, linear narrowing to obtuse apex, with spreading terete dorsal horn ± 1 mm long near base, fused to outer series near base, dark brown below becoming paler towards apices.

Distribution and habitat

Orbea knobellii is exclusively a species of the Kalahari 'desert' and it occurs fairly widely in southern Botswana, from Molepolole westwards to near Ghanzi as well as southwards to the vicinity of Upington and Griquatad in South Africa.

O. knobellii may be found growing in deep, fine sand among bushes and under these circumstances plants are widely scattered and fairly rare. It also occurs sometimes on low calcrete banks around pans among or under small *Acacia* bushes and other shrublets. In such cases it may become locally quite common.

Diagnostic features and relationships

Plants of *O. knobellii* may form substantial clumps up to 0.5 m across with quite densely packed stems. They also often have a few subterranean runners establishing new clumps some distance away from the parent, though

this rhizomatous habit mainly develops in plants growing in sand and is hardly present at all when specimens grow on hard, stony ground. The stems are stout and nearly square to concave between the four angles and they are pale green mottled with red-brown. They have quite stout, conical tubercles, each of which is tipped with a stout tooth that later becomes hard and ends in a sharpish, yellow tip. There are rarely any stipular denticles on the tubercles.

Flowers are produced in clusters near the base of the younger stems and open in rapid succession, often with two or three, but by no means all of the flowers on a cluster open at once. Although the stems look rather like those of *O. lutea*, the flowers are remarkably dissimilar. They are fairly small, at around 30 mm across, flat to somewhat reflexed, and have lots of irregular, purple-brown spots on a white to cream background. These spots are more or less round on the lobes and change gradually to narrow, concentrically arranged bars towards the centre. The spots are also variable in size on different plants: when they are large and coarse the flower may be quite dark whereas when they are fine it is nearly pure white. Inside, the surface is irregularly rugulose. The corolla becomes somewhat thickened towards the centre to form a very slight annulus which bounds a tiny tube containing the lower part of the corona.



Fig. 10.56. *O. knobellii*, PVB 3472, north of Upington.

As is usual, the outer corona lobes are broad and fairly short, with a ridged central zone on which some secretion takes place, leaving it darker than the rest. The inner lobes are slender and more or less erect but do not meet in the centre. Each of them has a slender and comparatively short, spreading dorsal horn.

History

Orbea knobellii was discovered by Johann Christian Knobel, a missionary and trader who lived for a time in Molepolole, Botswana, and probably collected it in the vicinity of the town around 1930.



Fig. 10.57. *O. knobellii*, PVB 3472, north of Upington, in habitat, January 1989.

ORBEA LUTEA

9. *Orbea lutea*

Orbea lutea (N.E. Br.) Bruyns, *Aloe* 37: 75 (2001).
Caralluma lutea N.E. Br., *Hooker's Icon. Pl.* 20:1.1901 (1890).

Orbeopsis lutea (N.E. Br.) L.C. Leach, *Excelsa Taxon.*

Ser. 1: 64 (1978).

Lectotype: South Africa, Cape, Griqualand, Klip-drift, Tuck sub MacOwan 2240 (K).

Succulent forming mat to 1 m diam. or more, occasionally rhizomatous. Stems 30-120 mm long, 10-25 mm thick (excluding teeth), decumbent, occasionally subterranean for short distances then erect above ground, grey-green mottled with red-brown; tubercles 6-10 mm long, usually joined into 4 broadly obtuse angles along stem with groove between angles, laterally flattened, tapering into conical to slightly laterally-flattened deltoid acute spreading tooth, usually with stipular denticles near apex. Inflorescence 1 (-2) per stem in lower half, of 3-30 flowers opening $\pm$ simultaneously from short peduncle, with several subulate bracts; pedicel 12-30 mm long, 3-4 mm thick; sepals 5-8 mm long, lanceolate to ovate-lanceolate, acuminate. Corolla 35-65 mm diam., rotate; outside smooth, pale cream-green; inside irregularly rugulose-papillate except in tube, uniformly yellow to red-brown or blotched with yellow on red-brown to nearly black; tube $\pm$ 2 mm deep, shallowly cupular, containing base of gynostegium, with corolla distinctly thickened around mouth; lobes 18-35 mm long, 6-15 mm broad at base, spreading, narrowly lanceolate, attenuate-acuminate, with vibratile clavate cilia along margins. Corona $\pm$ 6 mm tall, 10 mm broad, raised

slightly above base of tube on short pentagonal stipe < 1 mm long, red- to purple-brown or blackish sometimes with yellow edges to outer lobes; outer lobes $\pm$ 2 mm long, 3 mm broad, subquadrate, nearly contiguous so that 5 lobes almost appear to form cup with circular edge, with several radial slightly raised ridges on upper surface and darker with secretion between innermost of these, apex truncate-emarginate to toothed; inner lobes 0.8-1.0 mm long, adpressed to backs of anthers for at least half anthers' length but not exceeding anthers, towards base somewhat dorsiventrally flattened then narrowing and distinctly laterally flattened, with obtuse indistinct apex pressed to anthers, with erect and somewhat recurved dorsal horn (2.5-3.0 mm long) behind apex usually with smaller slender horn behind it, without dorsal gibbositities near base.

Orbea lutea is very widely distributed in southern Angola, Namibia, Botswana, the western corner of Zimbabwe as well as extensively in South Africa from near Pofadder in the west to KwaZulu-Natal. Two subspecies are recognised, one occurring on the western side of the sub-continent and the other further to the centre and to the east.

9a. *Orbea lutea* subsp. *lutea*

Caralluma lateritia N.E. Br., *Fl. Trop. Afr.* 4 (1): 486 (1903).

Caralluma lutea var. *lateritia* (N.E. Br.) Nel in A.C. White & B. Sloane, *Stap.*, ed. 2, 1: 373 (1937).

Type: Botswana, Ngamiland, Botletle Flats, Lugard 307 (K).

Caralluma vansonii Bremekamp & Obermeyer, *Ann. Transvaal Mus.* 16: 429 (1935).

Caralluma lutea var. *vansonii* (Bremek. & Oberm.) C.A. Lückh., *Stap.*: 62 (1952).

Type: Botswana, Nata River, Nkate, Van Son (PRE).

Caralluma lateritia var. *stevensonii* A.C. White & B. Sloane, *Stap.*, ed. 2, 1: 371 (1937).

Type: Zimbabwe, Wankie distr., Matetsi, Stevenson (missing).

Corolla inside often bright yellow or orange but sometimes dark red-brown speckled with yellow; lobes $\pm$ 3-5 (-7) times as long as broad, narrowly lanceolate, attenuated to acute point.

Key to the subspecies of *O. lutea*

- | | |
|--|-------------------------|
| Corolla lobes 1.5-2.5 times as long as broad | 9b. subsp. <i>vaga</i> |
| Corolla lobes $\pm$ 3-5 times as long as broad | 9a. subsp. <i>lutea</i> |

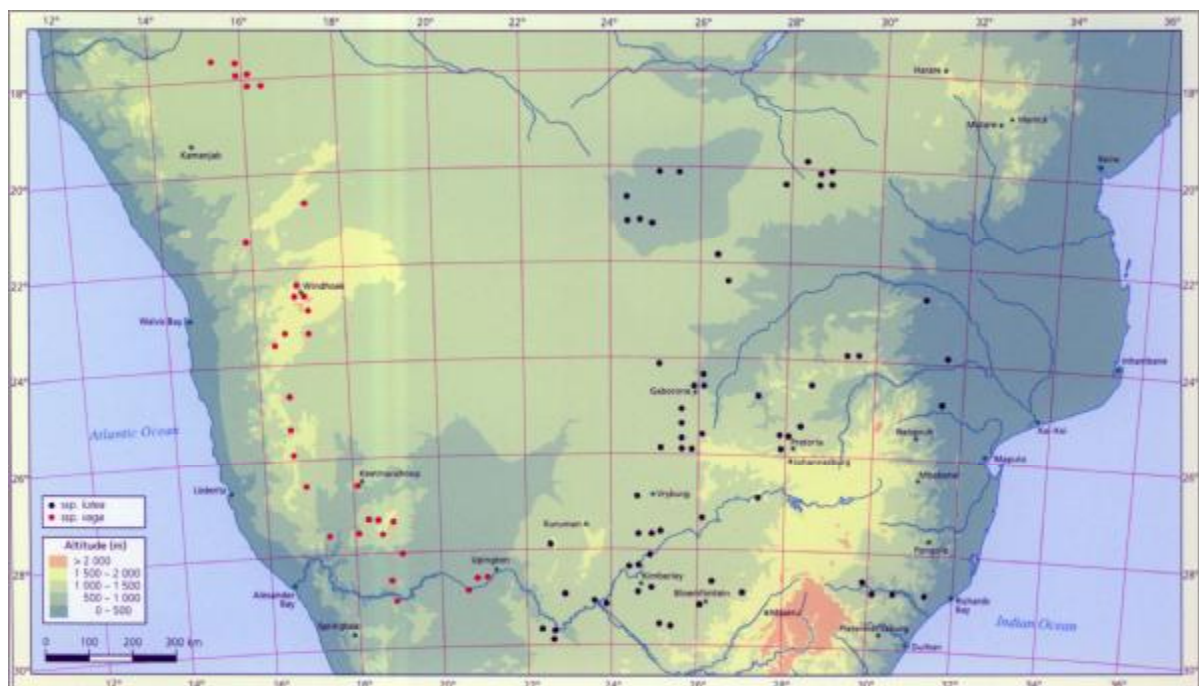


Fig. 10.58. Distribution of *Orbea lutea* in southern Africa.

Distribution and habitat

Subsp. *lutea* is widely distributed in South Africa in the former Cape Province from Prieska to Olifantshoek and Mafikeng, in the western Free State and widely north of the Vaal River, with an isolated patch between Ladysmith and Greytown in KwaZulu-Natal. In Botswana it is known around the low-lying area of the Mkari-kari Pans in the centre and in the south-east around Serowe and Gaborone. In Zimbabwe plants have been recorded from the area between Nyamandlovu and Bulawayo in the west.

Over this large area it occurs in a wide variety of habitats, often on calcrete or other stony outcrops. Plants are sometimes found under *Acacia* trees and sometimes among small grass clumps but are quite often to be seen growing in the open.

Diagnostic features and relationships

The stems of subsp. *lutea* are mostly more slender and have longer tubercles than the stout, shortly tubercled stems often seen in subsp. *vaga* and they also have more of a tendency to spread with underground runners.

The flowers are always extremely evil-smelling but are very variably coloured. In South Africa they are usually various shades of yellow, often very bright yellow and more rarely orange. In most of the material from Botswana flowers have a golden orange to pale reddish brown colour while in Zimbabwe they are red to dark maroon. Whereas unicoloured flowers predominate, others with fine yellow flecks on a darker background are occasionally found in Botswana and Zimbabwe. The corolla lobes are much narrower than in subsp. *vaga* and they are at least 3-5 (and even as much as 7) times as long as broad, gradually narrowing from a slightly ovate base to slender tips.

History

Subsp. *lutea* was first sent to Britain by John Sanderson 'from the Transvaal country' (Brown 1890) and his material flowered in March 1854 in the Natal Agricultural Society's garden. It was probably collected between November 1851 and April 1852. Other collections made by Mary E. Barber, William Tuck and Henry Barkly made their way to England and from these N.E. Brown was able to describe *Caraluma lutea* in 1890.



Fig. 10.59. *O. lutea* subsp. *lutea*, PVB 6519, north of Seokwane, Botswana, in habitat, December 1995.



Fig. 10.60. *O. lutea* subsp. *lutea*, PVB 4503a, west of Griquatstad.



Fig. 10.61. *O. lutea* subsp. *lutea*, north of Rakops, Botswana, in habitat, December 1995.

ORBEA LUTEA

9b. *Orbea lutea* subsp. *vaga*

Orbea lutea subsp. *vaga* (N.E. Br.) Bruyns, *Aloe* 37: 75 (2001).

Stapelia vaga N.E. Br., *Bull. Misc. Inform.* 1895: 265 (1895).

Caralluma vaga (N.E. Br.) A.C. White & B. Sloane, *Stap.*, ed. 2, 1: 381 (1937).

Orbeopsis lutea subsp. *vaga* (N.E. Br.) L.C. Leach, *Excelsa Taxon. Ser.* 1: 65 (1978).

Type: Namibia, Ovamboland, Olukonda, Schinz 2047 (K, holo.; Z, iso).

Caralluma nebrownii A. Berger, *Notizbl. Königl. Bot. Gart. Berlin* 4: 249 (1906).

Type: Namibia, Barmen, Dinter 1502 (K).

Caralluma brownii Dinter & A. Berger, *Deutsch-SWA Flora Forst- u. landwirtschaftliche Fragm.*: 113 (1909).

Type: unknown.

Caralluma pseudonebrownii Dinter, *Neue Pflanzen Deutsch-SWA's*: 17 (1914).

C. nebrownii var. *pseudonebrownii* (Dinter) A.C. White & B. Sloane, *Stap.*, ed. 2, 1: 377 (1937).

Type: Namibia, Keetmanshoop, Dinter 2598 (SAM).

Caralluma hahnii Nel in A.C. White & B. Sloane, *Stap.*, ed. 2, 3: 164 (1937).

Type: Namibia, Ovamboland, Ondonga (Ondangua?), Nel sub STE 7364 (missing).

Caralluma nebrownii var. *discolor* Nel in A.C. White & B. Sloane, *Stap.*, ed. 2, 3: 144 (1937).

Type: Namibia, Tsamap, Rusch sub STE 7366 (BOL).

Corolla blackish maroon to red-brown mottled finely with yellow (rarely yellow); lobes 1.5–2.5 times as long as broad, oblong-lanceolate, shortly acuminate.

Distribution and habitat

Subsp. *vaga* is found along more or less the whole length of Namibia, east of the Namib and west of the regions covered by Kalahari sands. It also extends into a small area of southwestern Angola adjacent to Ovamboland and continues southwards into South Africa, where it is known from west of Pofadder to near Upington.

Over this large area it occurs in a wide variety of habitats, from the firm, white sands of Ovamboland where it grows in the open or alongside *Acacia* trees, to rocky flats and slopes in the Great Karas Mountains under small bushes. Plants are also tolerant of a remarkable range of rainfall as well. Whereas much of Ovamboland receives 400–500 mm of rain per year, it can be found in arid areas with a low and unreliable average rainfall of less than 150 mm per year (as around Warmbad in southern Namibia). In arid areas such as the southernmost portion of Namibia and the Pofadder to Upington region of the northern Cape, it cohabits with other very resilient species such as *Hoodia gordonii* and *Larryleachia marlothii*.

Diagnostic features and relationships

Plants of subsp. *vaga* in Ovamboland have relatively narrow stems and a somewhat diffuse habit but in the drier parts of Namibia and South Africa the stems become thick and stoutly 4-angled, forming large and dense clumps. Very occasionally there are short subterranean stems but mostly the growth

is wholly superficial. The stems are usually brightly mottled with red-brown but in the north the mottling is pale and the whole stem is a fairly pale grey-green.

Flowers of *O. lutea* subsp. *vaga* are very striking. They are produced in dense clusters and vary from blackish maroon to red-brown, finely and very irregularly flecked with yellow. Yellow-flowered plants have been recorded (W. Giess, pers. comm.) but only very rarely. In general the corolla lobes are not more than 2.5 times as long as broad and therefore are much shorter than in most specimens of subsp. *lutea*.

There is little difference to be found between the two subspecies in the corona except that in subsp. *vaga* it is uniformly red-brown to blackish and often the outer lobes end in a small, central and sometimes bifid tooth.

History

Subsp. *vaga* was first collected in September 1885 by Hans Schinz near the Finnish Mission Station at Olukonda, south of Ondangua, where he stayed for some time. He also recorded it for the first time in Angola in 1885, when he travelled northwards from Olukonda to the Kunene at Onkumbi (Schinz 1891). In southern Namibia it was also recorded by Dinter in 1897, south of Keetmanshoop. There was a profusion of names for many of the early collections and Leach (1970b) reduced most of them to synonymy on the basis of the remarkable variation that he encountered among them during his travels in Botswana and northern Namibia.

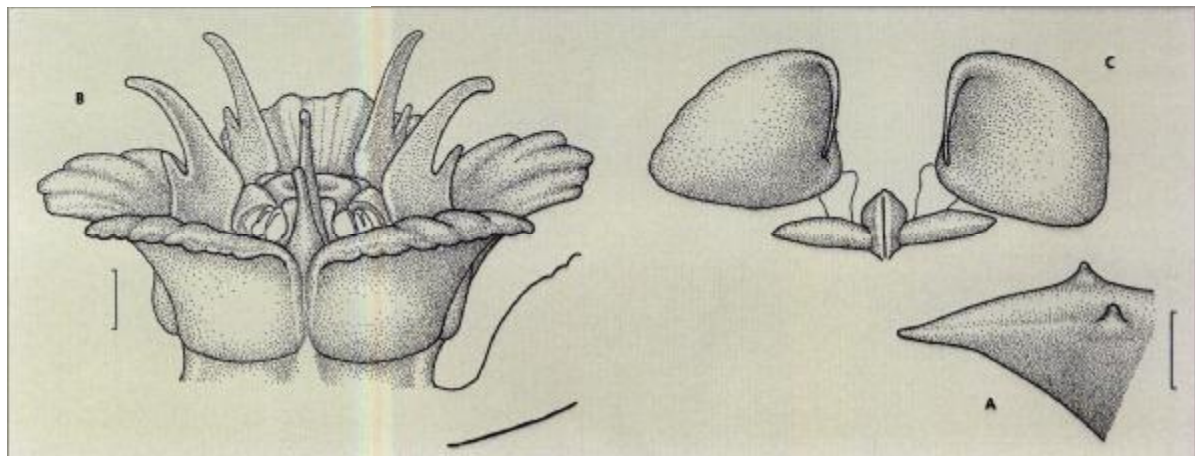


Fig. 10.62. *Orbea lutea* subsp. *vaga*. A, apex of tubercle. B, side view of gynostegium. C, pollinarium. Scale bars: A, 1 mm; B, 1 mm; C, 0.25 mm (at A). Drawn from: A, C, PVB 5231, Rosyebos, Pofadder; B, PVB 5750, Rooiwal, north of Grünau, Namibia.



Fig. 10.63. *O. lutea* subsp. *vaga*, PVB 4141, Nauchas, Namibia, in habitat, March 1993.



Fig. 10.64. *O. lutea* subsp. *vaga*, PVB 4141, Nauchas, Namibia, in habitat, March 1993.



Fig. 10.65. *O. lutea* subsp. *vaga*, PVB 3527, eastern side of the Great Karas Mountains, Namibia, in habitat, January 1989.



Fig. 10.66. *O. lutea* subsp. *vaga*, Eendorn, south-east of Warmbad, Namibia, in habitat, March 1993.

ORBEA GERSTNERI

10. *Orbea gerstneri*

Orbea gerstneri (Letty) Bruyns, *Aloe* 37: 74 (2001).

Caralluma gerstneri Letty, *Fl. Pl. South Africa* 16: t. 631 (1936).

Orbeopsis gerstneri (Letty) L.C. Leach, *Excelsa Taxon.*

Ser. 1: 66 (1978).

Type: South Africa, Natal, Magudu (Magut),

Gerstner 740 (PRE).

Small succulent forming dense clumps, often rhizomatous. Stems 30-100 mm long, 5-20 mm thick (excluding teeth), slender to stout, decumbent, dark grey-green to dark

green mottled with red-purple; *tubercles* 4-13 mm long, arranged into 4 obtuse rows along stem, tapering into laterally flattened deltoid acute spreading to ascending tooth rarely with 2 minute denticles on either side towards apex. *Inflorescence* 1 (-3) per stem from base to near apex, of 3-8 flowers opening $\pm$ simultaneously or in succession from short peduncle (< 2 mm long), with several subulate laterally toothed bracts 2.0-2.5 mm long; *pedicel* 6-10 mm long, 2.0-2.5 mm thick, ascending and holding flowers facing upwards or horizontally; *sepals* 5-8 mm long, 1.5-2.0 mm broad at base, lanceolate, acuminate. *Corolla* 35-60 mm diam., rotate-campanulate; outside smooth, finely mottled with purple-red on pale

Key to the subspecies of *O. gerstneri*

Stems slender and very rhizomatous, tubercles arranged loosely into 4 rows

along stem, corolla tube 5-6 mm long, outer corona lobes 2.0-3.5 mm long **10a. subsp. *gerstneri***

Stems stout and occasionally rhizomatous, tubercles joined into 4 angles

along stem, corolla tube 7-9 mm long, outer corona lobes 5-6 mm long **10b. subsp. *elongata***

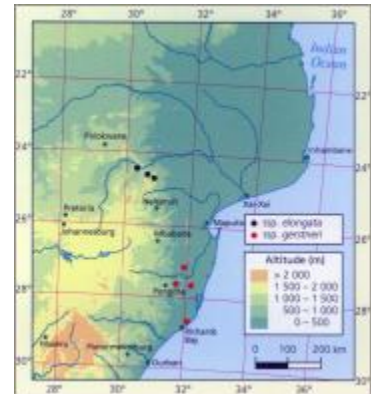


Fig. 10.67. Distribution of *Orbea gerstneri*.

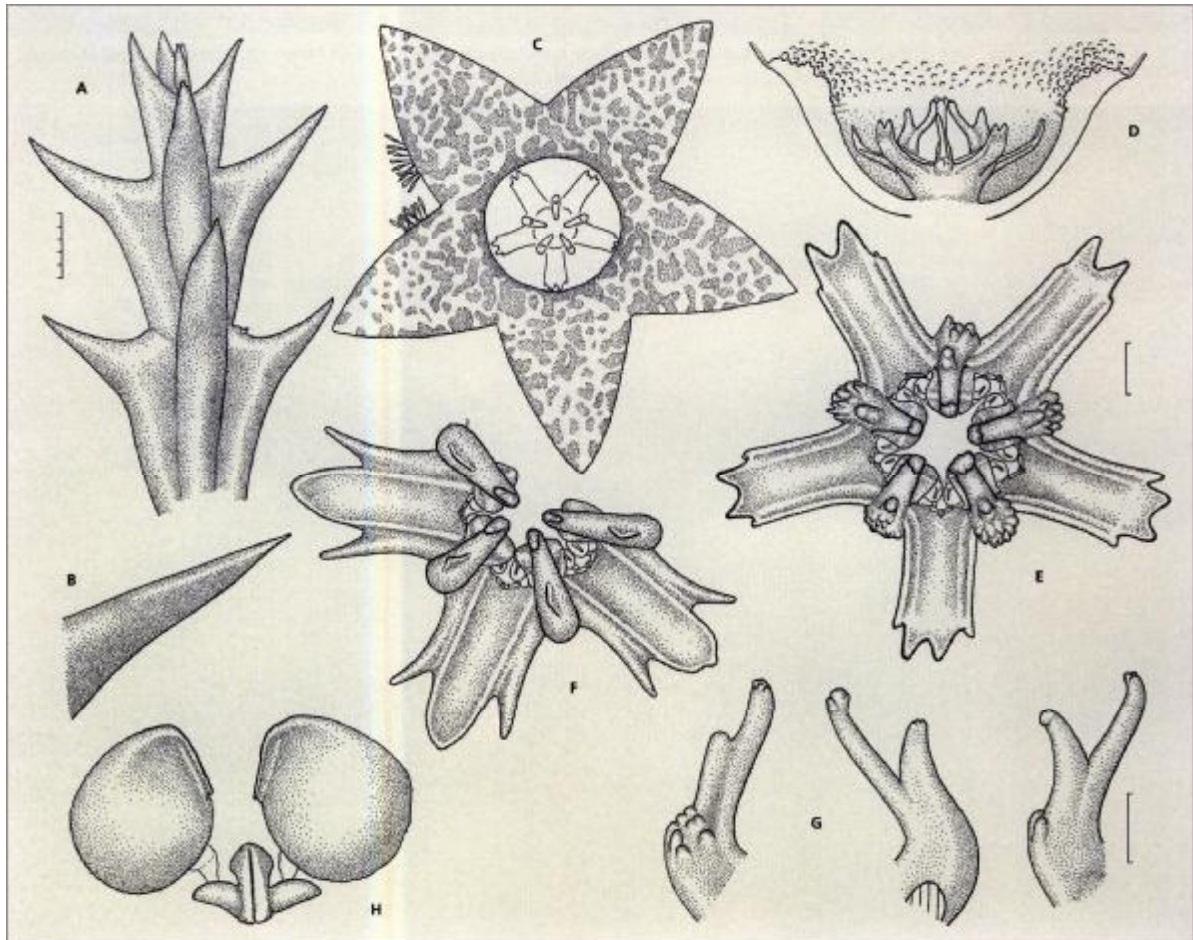


Fig. 10.68. *Orbea gerstneri* subsp. *gerstneri*. A, apex of stem. B, apex of tubercle. C, face view of flower. D, side view of centre of dissected flower. E, F, face view of gynostegium (or part). G, side view of inner corona lobe from different flowers. H, pollinarium. Scale bars: A, C, 5 mm (at A); B, 2 mm (at A); D, 3 mm (at G); E, F, 1 mm (at E); G, 1 mm; H, 0.25 mm (at G). Drawn from: A, B, F, PVB 4454, Mkuzi; rest, *De Kock & Bayer* 352, Nseleni.

cream-green to pale cream-green towards base; inside dark purple-red mottled with cream becoming solid purple-brown in tube, irregularly rugulose-papillate with rugosities disappearing in lower half of tube, rugosities somewhat organised into longitudinal lines on lobes; *tube* 6-8 mm long, 10 mm broad, cupular, pentagonal, with corolla slightly thickened at mouth and sometimes with raised annulus there; *lobes* 11-17 mm long, 7-10 mm broad at base, spreading, slightly ovate, deltate to lanceolate, acute, flat above, with clavate vibratile cilia 1.5-2.0 mm long along margins of lower third. *Corona* 4.0-4.5 mm tall, 9.0-9.5 mm broad, raised above base of tube on short stipe ($\pm$ 1 mm long), red-brown; *outer lobes* 2-3 mm long, 1.5-2.0 mm broad, $\pm$ rectangular, spreading with ascending tips, with 2 raised radial ridges on upper surface (area between them dark purple-brown), apex deltoid to bifid between these ridges outside them truncate to attenuated into spreading lobules; *inner lobes* 2.5-3.0 mm long, with lower slightly dorsiventrally flattened portion adpressed to backs of anthers for half anthers' length then becoming $\pm$ terete and ascending-connivent with slender to clavate-tuberculate apex, with dorsal (slightly laterally flattened) horn about halfway up lobe, dorsal gibbosity/hornlets at base partly fused to outer series, brown.

Orbea gerstneri is a poorly known species and has been regarded as rare (Leach 1978a). The considerable corolla tube (which is entirely lacking in the previous two species) suggests that it is closely allied to *O. huillensis* and *O. valida* and also separates these three species from all others previously placed in *Orbeopsis*. The very large stems with especially prominent stipular denticles that are usually seen in the latter two cannot be confused with the comparatively small stems in *O. gerstneri*, which rarely have any stipular denticles at all and are also usually a peculiar and characteristic dark green colour (they are always paler green in *O. huillensis* and *O. valida*). Although the shape of the flower is similar in all these species, the corolla lobes are flat above in *O. gerstneri* while they are always distinctly convex above in *O. huillensis* and *O. valida*. There are some differences in the respective coronas: the inner corona lobes of *O. gerstneri* are cylindrical above with a slightly thickened tip and the dorsal projection extends upwards along the lobe for some distance (in *O. huillensis* and *O. valida* the lobes are mostly distinctly flattened above and the dorsal projection is restricted to the base of the inner lobe).

The two subspecies of *O. gerstneri* have very different stems and these differences are similar to those seen between the stems of *O. cooperi* and *O. tapscottii* or *O. maculata* subsp. *maculata* and subsp. *rangeana*. Nevertheless, the flowers differ mainly in the longer corolla tube and corolla lobes of subsp. *elongata*.

This species is found along the north-eastern escarpment of South Africa, in eastern Swaziland and in northern KwaZulu-Natal.

10a. *Orbea gerstneri* subsp. *gerstneri*

Dwarf succulent forming several often small clumps (30-100 mm diam.) joined by rhizomes. Stems 30-70 mm long, 5-7 mm thick (excluding teeth), $\pm$ slender, decumbent and often subterranean for some distance (up to 300 mm) then erect above ground; *tubercles* 4-13 mm long, arranged loosely into 4 obtuse rows along stem $\pm$ without groove between them, tapering into prominent horizontally spreading to ascending slender laterally flattened deltoid acute tooth. *Corolla* 35-40 mm diam.; *tube* 5-6 mm long, 10 mm broad, pentagonal. *Outer corona lobes* 2.0-3.5 mm long, spreading with ascending tips.

Distribution and habitat

Subsp. *gerstneri* is known from only a few collections and has been gathered in a relatively small area from Ingwavuma in Swaziland southwards to Magudu, Mkuzi and near Ulundi in the northern part of KwaZulu-Natal.

It generally seems to grow in low-lying areas at altitudes of 250-700 m in flat, sandy to stony ground.

Diagnostic features and relationships

In subsp. *gerstneri* the stems have a strongly rhizomatous habit, with slender runners spreading underground for up to 300 mm. As a consequence one may find clumps of stems spread out over an area of 1 sq m or more that are connected underground into a single plant. The stems are fairly slender, with long, narrowly deltoid tubercles arranged loosely into four rows along the stem: in short, more or less identical to those of *O. maculata*. However, they are an altogether darker green than the stems of *O. maculata*.

Florally subsp. *gerstneri* and *O. maculata* are very different. In subsp. *gerstneri* the flowers are produced in small, simultaneously

opening clusters of up to six but usually four or fewer. They are short-lived, lasting for only one to three days and emit a dreadful, excrement-like stench. Outside they are finely, reticulately mottled with purple-red on pale green and inside these colours are intensified to a richness and patterning rivaling that of an intensely coloured Persian carpet. In the centre of the flower there is a short cupular tube which is usually about half as long as broad, with a pentagonal mouth and a dark purple-brown colour within. The inside is densely and reticulately rugulose (which further intensifies the richness of the colours) and there are, in addition, smaller papillae which encrust these rugosities on the surface and which have somewhat different shapes in the two subspecies. The general ornamentation is completed by a fringe of small, dark, shiny and vibratile, clavate cilia near the bases of the lobes.

In subsp. *gerstneri* the corona is clearly visible from outside the flower. The outer corona lobes spread out on the base and up the side of the tube. They have a channelled inner area which becomes wet with secretion of nectar and is much darker than the almost reddish margins. These margins are sometimes extended into additional small, spreading teeth. As the accompanying illustrations (fig. 10.68 G) show, the inner lobes are very variable in length, in the number of dorsal projections and in the length of these projections relative to the length of the lobe.

History

Subsp. *gerstneri* was discovered in northern KwaZulu-Natal by the missionary F. Jacob Gerstner just outside the mission at Magudu (Magut) apparently in February 1936. It was next collected in Cecil Mack's Pass in Swaziland by Roy DA. Bayliss in July 1962. The other two known collections were made more recently.



Fig. 10.69. *O. gerstneri* subsp. *gerstneri*, PVB 4454, Mkuzi.

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10b. *Orbea gerstneri* subsp. *elongata*

Orbea gerstneri subsp. *elongata* (R.A.Dyer)

Bruyns, *Aloe* 37: 74 (2001).

Caralluma gerstneri subsp. *elongata* R.A.Dyer, *Fl. Pl. Africa* 40:1.1567 (1969).

Orbeopsis gerstneri subsp. *elongata* (R.A.Dyer)

L.C. Leach, *Exceisa Taxon. Ser. 1*: 67 (1978).

Type: South Africa, Transvaal, Penge, *Phillips sub PRE 30367* (PRE).

Succulent forming clump 100 mm to 1 m diam. Stems 30-100 mm long, 6-20 mm thick (excluding teeth), stout, sometimes rhizomatous for up to 100 mm; *tubercles* 4-9 mm long, joined into 4 obtuse angles along stem with slight to broadly concave groove between angles, tapering into spreading deltoid acute laterally flattened tooth sometimes with fine ascending denticles near apex. Corolla 35-60 mm diam.; tube 7-9 mm long, 8-9 mm broad, pentagonal to circular at mouth but distinctly pentagonal towards base with sepals resting on vertices of pentagon outside, inside with small translucent-white



Fig. 10.70. *O. gerstneri* subsp. *elongata*, PVB 6605, north-east of Ohrigstad.

papillae on otherwise purple-brown background, corolla thickened around mouth sometimes into slightly raised annulus; lobes sometimes becoming greenish towards tips. *Outer corona lobes* 5-6 mm long, steeply ascending against sides of corolla tube.

Distribution and habitat

Subsp. *elongata* occurs at elevations of 900-1600 m in the mountains of the north-eastern escarpment of South Africa along the Olifants River and its tributary the Blyde River. Until recently it was known only from the type locality at Penge. It also grows on slopes and hilltops along the western side of the Blyde River Canyon some 60 km south-east of the type locality.

This subspecies also grows in stony places but here the plants are wedged among stones and clumps of grass on hillsides, often on soils derived from dolomite.

Diagnostic features and relationships

In plants of subsp. *elongata* the stems are tightly packed into clumps which often reach 300 mm across but may achieve 1 m in diameter occasionally. The plants are not entirely without

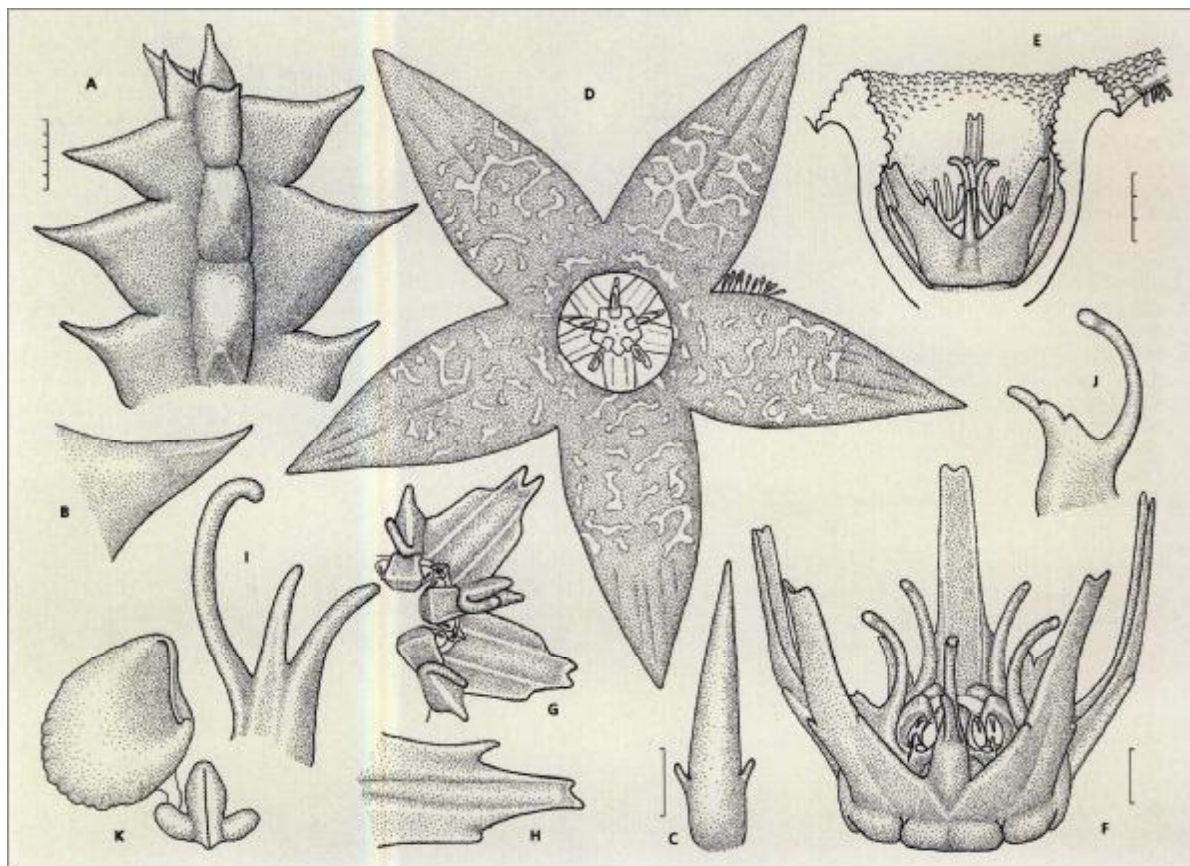


Fig. 10.71. *Orbea gerstneri* subsp. *elongata*. A, apex of stem. B, apex of tubercle. C, bract from inflorescence. D, face view of flower. E, side view of centre of dissected flower. F, side view of gynostegium. G, face view of part of gynostegium. H, face view of outer corona lobe. I, J, side view of inner corona lobe. K, pollinarium. Scale bars: A, D, 5 mm (at A); B, 2 mm (at C); C, I, J, 1 mm (at C); E, 3 mm; F, G, H, 1 mm (at F); K, 0.25 mm (at C). Drawn from: A, B, PVB 6601, north-east of Ohrigstad; C, D, F, G, J, PVB 2042, Penge; E, H, I, K, PVB 6605, north-east of Ohrigstad.

underground runners but, as with the stems, these tend to be shorter and thicker than those found in subsp. *gerstneri*. The stems are stout and comparatively short, with broadly deltoid tubercles. They are dark green to brownish, flecked with purple if exposed, and are very similar in colour to those of subsp. *gerstneri*.

Florally the two subspecies are very similar. In subsp. *elongata* the lobes are less variable in length and are generally at least twice as long as broad, whereas in subsp. *gerstneri* they may sometimes be quite short. In subsp. *elongata* the tube is mostly deeper than broad and it is sufficiently long that the gynostegium is somewhat hidden in it. The outer corona lobes are also considerably longer and usually rise nearly to the mouth of the tube.

History

Subsp. *elongata* was discovered by CT. Phillips in the hills above the now defunct and abandoned asbestos mine at Penge, sometime just before 1969.



Fig. 10.72. *O. gerstneri* subsp. *elongata*, PVB 6605, north-east of Ohrigstad. In this flower a small raised annulus is visible around the mouth of the corolla tube.



Fig. 10.73. *O. gerstneri* subsp. *elongata*, PVB 7019, near Blyde River Canyon.



Fig. 10.74. *O. gerstneri* subsp. *elongata*, PVB 2042, Penge.

Key to the subspecies of *O. huillensis*

Stems without underground rhizomes, 20–30 mm thick (excluding teeth), corolla inside brown to maroon	11a. subsp. <i>huillensis</i>
Stems with underground rhizomes, 15–20 mm thick (excluding teeth), corolla inside yellow	11b. subsp. <i>flava</i>

11. *Orbea huillensis*

Orbea huillensis (Hiern) Bruyns, *Aloe* 37: 74 (2000).

Caralluma huillensis Hiern, *Cat. Afr. Pl.* 1 (3): 697 (1898).

Orbeopsis huillensis (Hiern) L.C. Leach, *Excelsa*

Taxon. Ser. 1: 68 (1978).

Type: Angola, Huila, Welwitsch 4266 (BM, holo.: LISU, iso.).

Succulent forming diffuse to dense clump 150 mm–3 m diam., sometimes rhizomatous. Stems 40–300 (–500) mm long, 15–30 mm thick (excluding teeth), usually massive, decumbent, grey-green usually marbled with red-purple; tubercles 5–25 mm long, joined into 4 (rarely 5) continuous often narrowly obtuse wing-like angles along stem with deep groove between angles, laterally flattened, forming prominent to very large deltoid spreading acute tooth with 2 denticles near tip (tip gradually becoming hardened and covered with yellowish corky layer). Inflorescences 1–3 per stem (younger ones only) from base to near apex, each of 5–40 extremely smelly flowers opening ± simultaneously from stout cylindrical truncate peduncle (± 15 mm long, 5–10 mm thick); pedicels 10–45 mm long, 2–3 mm thick, horizontal to ascending, with slender lanceolate laterally toothed bracts 4–8 mm long at base; sepals 5–9 mm long, 2–3 mm broad at base, ovate-lanceolate, acuminate with recurved tips. Corolla 55–85 mm diam., ± rotate, deeply lobed; outside smooth, purplish to pale pink on lobes to cream towards base of tube; inside dark brown, maroon, dark purple or yellow, transversely papillate-rugulose; tube 5–7 mm deep, cupular, usually completely containing gynostegium, corolla somewhat thickened at mouth; lobes 20–45 mm long, 5–9 mm broad at base, spreading, ovate-lanceolate, narrowly attenuate, convex from reflexed margins, with scattered maroon to white vibratile clavate to spatulate cilia up to 3 mm long along margins or eciliate. Corona 3.5–4.5 mm tall, 5.5–8.0 mm broad, raised above base of tube by stout pentagonal stipe 1.0–1.5 mm long, deep purple-brown to orange (in yellow flowers); outer lobes 1.5–3.0 mm long, 1.5–2.5 mm broad, spreading to ascending, usually with several radial ridges along inner face some of which extend into various apical teeth, oblong acute to truncate-dentate or deltoid, laterally fused towards base to lower sides of inner lobes; inner lobes 1.5–3.5 mm long, adpressed to backs of anthers then ascending and usually recurved towards apices, linear, dorsiventrally flattened sometimes only very slightly, becoming terete above, obtuse to slightly bifid apically, base swollen dorsally above outer lobes into rounded boss or produced into series of spreading teeth.

Leach (1965) was the first to provide any illustrations of *Caralluma valida* and *C. gossweileri*. He later (Leach 1970b) wrote about them again and this time he included a discussion of *C. huillensis* and *C. tsumebensis* and suggested that *C. huillensis* and *C. gossweileri* and possibly also *C. tsumebensis* may prove to be conspecific.

At that stage Leach was hesitant, because of the paucity of material that he had seen, to take as broad a view of this complex as he did in the complex surrounding *Caralluma lutea* where 'not to have followed this policy would have resulted in the recognition of almost innu-

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merable taxa, since it seems that within some species, not only are no two specimens identical but that the range of variation within even small populations may be almost unbelievably wide'. (Leach 1970b:157). Investigations of this complex have revealed the existence of four elements, two of which were known to Leach (corresponding to the *C. gossweileri* and *C. valida* of Leach (1965)) and two of which have only been discovered since 1990. As was already suggested (Leach 1970b), it has proven impossible to separate *C. gossweileri*, *C. huillensis* and *C. tsumebensis* and these three are considered to belong to a single taxon, for which the earliest valid specific epithet is '*huillensis*'.

In the present account two species, *O. huillensis* and *O. valida*, are recognised. *Orbea huillensis* is now known to be considerably more variable than before with yellow to maroon or brown flowers which sometimes bear cilia along the margins of the lobes: in all of them, however, the flowers are greater than 55 mm in diameter and have narrowly attenuate corolla lobes. Both rhizomatous and non-rhizomatous forms are known.

Orbea huillensis is found in southern Angola, southern Zambia, Namibia east of Grootfontein, in the north-western corner of Botswana and in western Zimbabwe. It is distinguished from *O. valida* by the size of the corolla and the narrowly attenuate corolla lobes.

Many plants of *O. huillensis* and *O. valida* have exceptionally robust stems, in which case it is easy to separate them from the ubiquitous *O. lutea*. However, in more slender-stemmed plants it is usually the noticeably larger stipular denticles, which are up to 2 mm long, that suggests that one is dealing with a member of this complex rather than with *O. lutea*, where the stipular denticles are barely visible, if at all. Florally, neither *O. huillensis* nor *O. valida* is easily confused with *O. lutea*. Both *O. huillensis* and *O. valida* have flowers with a distinct corolla tube in the centre. The respective coronas differ in that the outer lobes of *O. lutea* are much broader than is ever seen in either *O. huillensis* or *O. valida* and the inner lobes in *O. lutea* consist almost entirely of the dorsal projection whereas in *O. huillensis* and *O. valida* the dorsal projection is confined to the base of the lobe.

11a. *Orbea huillensis* subsp. *huillensis*

Caralluma gossweileri S.Moore, J. Bot. 50: 367 (1912).

Orbeopsis gossweileri (S.Moore) L.C.Leach, Excelsa

Taxon. Ser. 1:67(1978).

Type: Angola, Forte Princeza Amelia (near Kuvango), Gossweiler 2098 (BM, holo.; COL, K, iso.).

Caralluma tsumebensis Oberm. in A.C. White & B.

Sloane, Stap., ed. 2, 3:1163 (1937).

Orbeopsis tsumebensis (Oberm.) L.C.Leach, Excelsa

Taxon. Ser. 1:68(1978).

Type: Namibia, cultivated specimen, Tsumeb, Nägelsbach sub Transvaal Mus. 32820 (PRE).

Succulent forming diffuse to dense clumps up to 3 m diam. Stems 40-300 mm long, 20-30 mm thick (excluding teeth), usually massive, without underground rhizomes; tubercles (10-) 15-25 mm long. Corolla 55-85 mm diam.; inside dark brown to deep maroon. Corona deep purple-brown.

Distribution and habitat

Subsp. *huillensis* is found in southern Angola, north-western Botswana, southern Zambia and western Zimbabwe and it is particularly widespread in northern Namibia east of Grootfontein.

Plants usually grow in the shelter of small trees and are more rarely found in the open. They usually occur on fine white to black sand, sometimes where it overlays calcrete.



Fig. 10.75. *O. huillensis* subsp. *huillensis*, PVB 6480, Kangwa, Botswana.



Fig. 10.76. *O. huillensis* subsp. *huillensis*, PVB 5525, south-west of Grootfontein, Namibia. The larger stems here are nearly 30 cm tall and plants up to 3 m in diameter were found at this spot, February 1993.

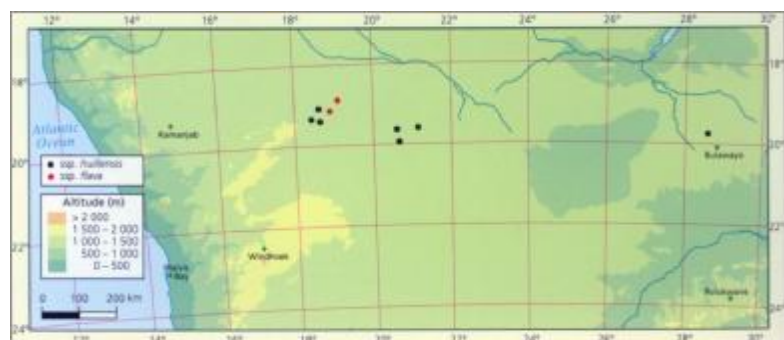


Fig. 10.77. Distribution of *Orbea huillensis* in southern Africa.

Diagnostic features and relationships

Plants of subsp. *huillensis* often form clumps covering over 1 sq m in area but enormous specimens up to 3 m in diameter have been seen. They have extremely robust stems (up to 500 mm tall and 80 mm across, if one includes the teeth), with very large deltoid teeth along the angles and they exhibit no tendency to form

subterranean runners at all.

The flowers vary considerably in diameter and are usually deep maroon to deep brown. They have slender, attenuate lobes and a cupular tube 5-7 mm deep which contains the gynostegium completely. On plants in Namibia and Botswana some flowers have a few cilia along the margins of the lobes but most are completely without them.

The outer corona lobes are short, more or

less rectangular and spreading, but they are extremely variable in outline and also especially in the ridges and furrows on the upper surface. The inner lobes are relatively slender, slightly flattened to nearly terete, initially adpressed to the backs of the anthers then rising more or less vertically above them and sometimes connivent in a column in the centre. They always have a low, swollen and rounded dorsal projection in series with the outer lobes.

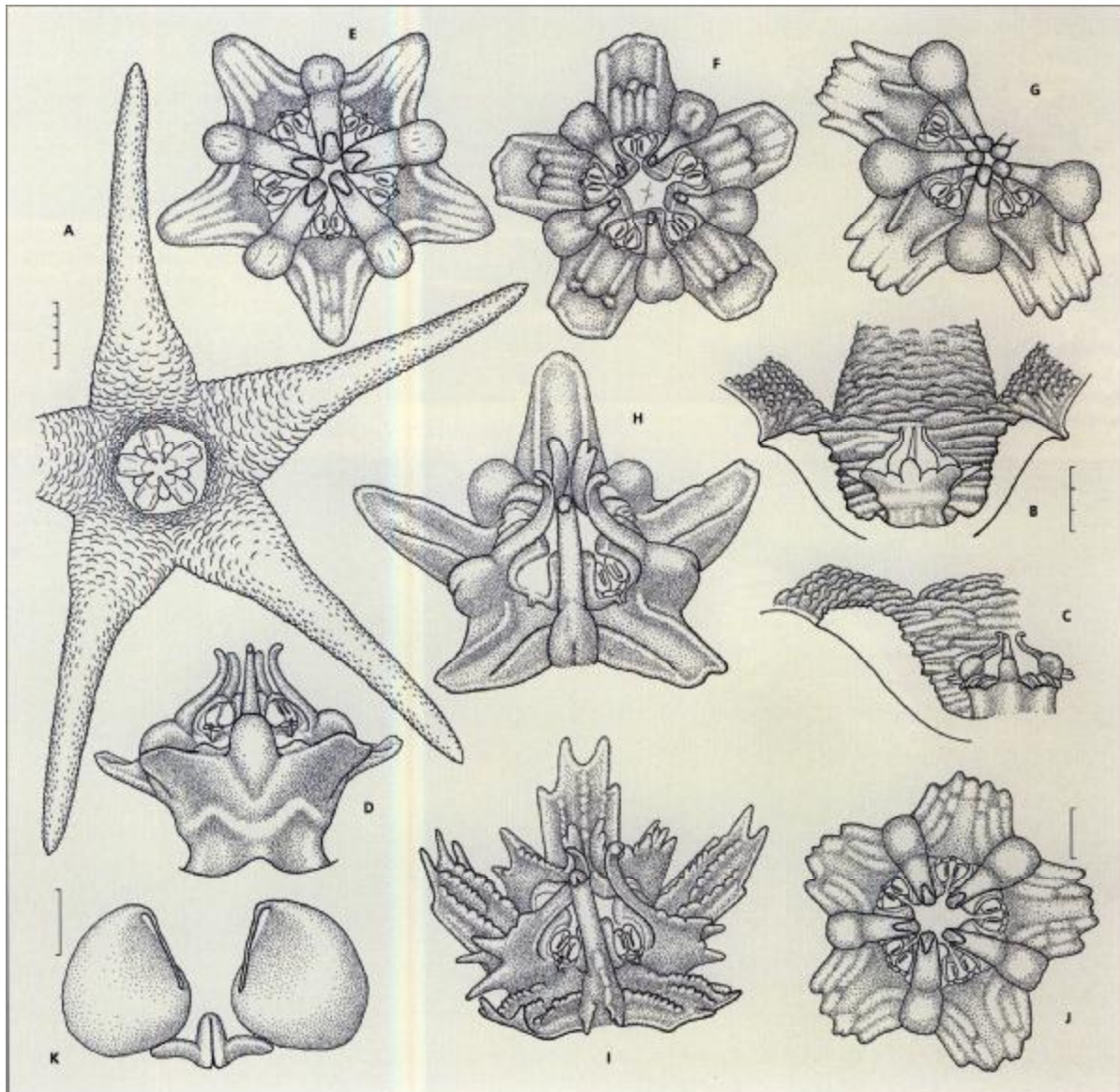


Fig. 10.78. *Orbea huillensis*. (A-G, subsp. *huillensis*; H, I, subsp. *flava*) A, face view of flower. B, C, side view of centre of dissected flower. D, side view of gynostegium. E-J, face view of gynostegium. K, pollinarium. Scale bars: A, 5 mm; B, C, 3 mm (at B); D-J, 1 mm (at J); K, 0.25 mm. Drawn from: A, B, D, F, K, PVB 4133, north-east of Grootfontein, Namibia; C, J, PVB 6480, Kangwa, Botswana; E, G, PVB 5525, east of Grootfontein, Namibia; H, I, PVB 5522, north-east of Grootfontein, Namibia.

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History

Caralluma huillensis was discovered, in flower, by Friedrich Welwitsch near Huila in southern Angola in December 1859. *Caralluma gossweileri* was collected by John Gossweiler before 1912, but he regarded this merely as *C. huillensis*, making the remark 'surely = *C. huillensis*'

on the type sheet. The next record of this species is the specimen collected in Zimbabwe under the number *Plowes i884*, which flowered in 1953 and remains the only collection known from Zimbabwe. Another record was made in Angola in 1955 by Santos. Since then records have very slowly accumulated but they remain few in number.



Fig. 10.79. *O. huillensis* subsp. *huillensis*, PVB 4133, north-east of Grootfontein, Namibia.

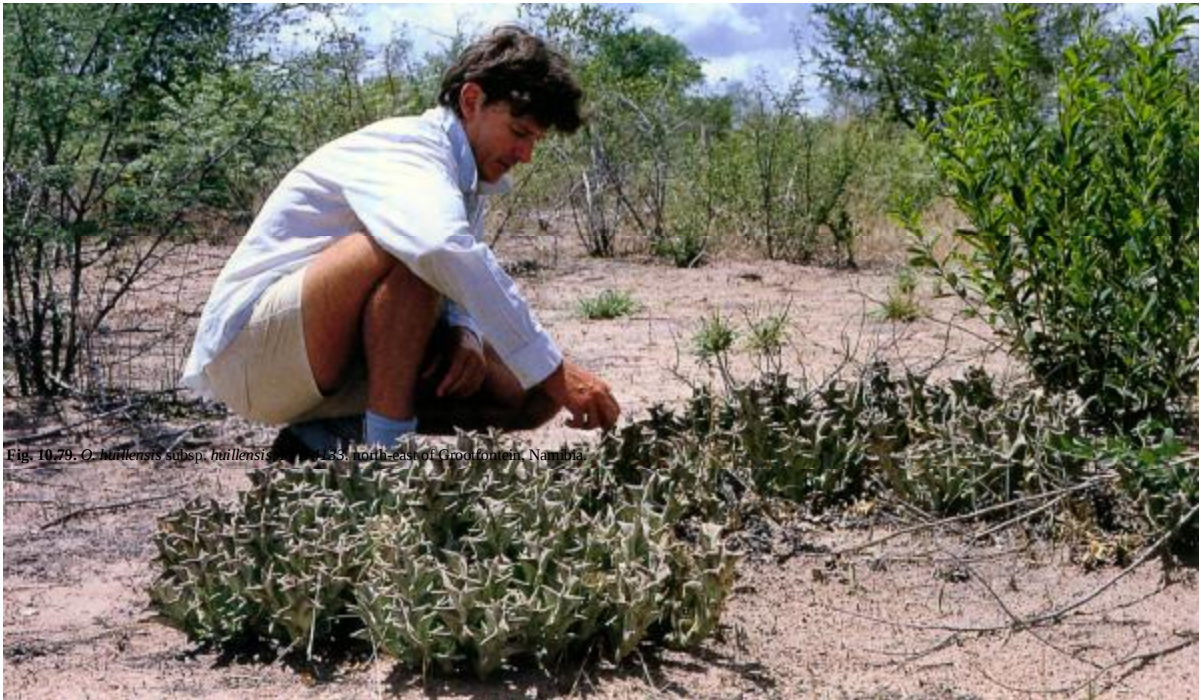


Fig. 10.79. *O. huillensis* subsp. *huillensis*, PVB 4133, north-east of Grootfontein, Namibia.

Fig. 10.80. *O. huillensis* subsp. *huillensis*, PVB 4126, south-east of Tsumkwe, Namibia This medium-sized specimen, being examined by Clive R. McDowell, extended over about 2 square meters, January 1990.

11. *Orbea huillensis* subsp. *flava*

Orbea huillensis subsp. *flava* Bruyns, *Aloe* 37: 76 (2001).

Type: Namibia, north-east of Grootfontein, Bruyns 5522 (BOL).

Succulent forming diffuse clump 150-300 mm diam. Stems 40-120 mm long, 15-20 mm thick (excluding teeth), relatively slender, often with underground rhizomes; tubercles 5-15 mm long. Corolla 70-85 mm diam.; inside yellow. Corona orange.

Distribution and habitat

Subsp. *flava* is known only in the north-eastern corner of Namibia, north-east of Grootfontein.

Plants are found in this area in open forest with *Terminalia sericea* and other trees on pale, whitish sands.

Diagnostic features and relationships

In subsp. *flava* the stems are grouped into relatively small clumps and often produce underground rhizomes. They are also considerably smaller (both more slender and shorter) and less boldly toothed than those of subsp. *huillensis*.

Florally the two subspecies are only distinguishable by the different colours of



Fig. 10.81. *O. huillensis* subsp. *flava*, PVB 5522, north-east of Grootfontein, Namibia.

their flowers: the corolla is yellow in subsp. *flava* and the corona is orange. Here the corolla has not been found to vary much in size and is generally large with plenty of vibratile cilia along the margins of the lobes. In subsp. *flava* the inner corona lobes are much longer than in subsp. *huillensis* and are usually somewhat bifid apically. Some remarkable variation has been observed in the shape of the excrescences near the base of the inner lobes and some of this variation is shown in fig. 10.78. These have been seen to vary from the swollen, round shape that is typical of subsp. *huillensis* to remarkable, rather more flattened structures consisting of

several, spreading, acute teeth. This variation just serves to indicate how cautiously one should treat these structures taxonomically.

History

This subspecies was first recorded by Ben Strohbach, of the National Herbarium, Windhoek, Namibia, while doing a survey north-east of Grootfontein in 1991. In 1993 a few plants were located on the same farm where he had found it as well as more on another farm some 20 km to the north-east. There are no other known records of it.



Fig. 10.82. *O. huillensis* subsp. *flava*, PVB 5522, north-east of Grootfontein, Namibia, in habitat, February 1993.

12. *Orbea valida*

Orbea valida (N.E. Br.) Bryuns, *Aloe* 37: 76 (2001).
Caralluma valida N.E. Br., *Bull. Misc. Inform.* 1895: 264 (1895).
Orbeopsis valida (N.E. Br.) L.C. Leach, *Excelsa Taxon. Ser.* 1: 67 (1978).
 Type: ? Botswana, Holub (K).

Succulent forming diffuse clump 80-750 mm diam., sometimes rhizomatous. *Stems* 40-200 mm long, 15-25 mm thick (excluding teeth), usually massive, decumbent, grey-green usually marbled with red-purple; *tubercles* 5-25 mm long, joined into 4 (rarely 5) continuous often narrowly obtuse wing-like angles along stem with deep groove between angles, laterally flattened, forming prominent to very large deltoid spreading acute tooth with 2 denticles near tip (tip gradually becoming hardened and covered with yellowish corky layer). *Inflorescences* 1-3 per stem (younger ones only) from base to near apex, each of 5-40 extremely smelly flowers opening $\pm$ simultaneously from stout cylindrical truncate peduncle ($\pm$ 15 mm long, 5-10 mm thick); *pedicels* 10-45 long, 2-3 mm thick, horizontal to ascending, with slender lanceolate laterally toothed bracts 4-8 mm long at base; *sepals* 5-9 mm long, 2-3 mm broad at base, ovate-lanceolate, acuminate with recurved tips. *Corolla* 35-45 (-55) mm diam., $\pm$ rotate, deeply lobed; outside smooth, purplish to pale pink on lobes to cream towards base of tube; inside deep maroon to pinkish red, transversely papillate-rugulose; *tube* 2-6 mm deep, cupular to shallowly cupular, mostly completely containing gynostegium, with corolla somewhat thickened at mouth; *lobes* 15-20 (-25) mm long, 5-9 mm broad at base, spreading, ovate-lanceolate, narrowly attenuate, convex from reflexed margins, with scattered maroon to white vibratile clavate to spatulate cilia up to 3 mm long along margins. *Corona* 3.5-4.5 mm tall, 5.5-8.0 mm broad, raised above base of tube by stout pentagonal stipe 1.0-1.5 mm long, deep purple-brown; *outer lobes* 1.5-3.0 mm long, 1.5-2.5 mm broad, spreading to ascending, usually with several radial ridges along inner face some of which extend into various apical teeth, oblong acute to truncate-dentate or deltoid, laterally fused towards base to lower sides of inner lobes; *inner lobes* 1.5-3.5 mm long, adpressed to backs of anthers then ascending and usually recurved towards apices, linear, dorsiventrally flattened sometimes only very slightly, becoming terete above, obtuse to slightly bifid apically, base swollen dorsally above outer lobes into rounded boss or produced into series of spreading teeth.

Orbea valida has been recorded in north-eastern Namibia, northern Botswana, southern Zambia and western Zimbabwe.

Here, as in the case of *O. huillensis*, a broader view of *O. valida* is taken. In this species there are always cilia along the margins of the lobes and the flower is 35-45 mm in diameter, with narrowly deltate lobes. Furthermore the pollinia are always much broader than long whereas they are almost exactly as long as broad in *O. huillensis*. In *O. valida* the corolla tube is very variable in depth (far more so than has been observed in *O. huillensis*) and the corona is also variable so that in some cases

ORBEA VALIDA

it may look just like that of *O. huillensis*. Very rhizomatous plants are found in the western part of the range and these have a more than usually shallow corolla tube.

12a. *Orbea valida* subsp. *valida*

Succulent forming diffuse to dense clump up to 1 m diam. Stems 40-200 mm long, 20-25 mm thick (excluding teeth), massive, without underground rhizomes; *tubercles* (10-) 15-25 mm long. *Corolla* 35-45 (-55) mm diam.; inside deep maroon to dark purple-red; *tube* 5-6 mm deep, cupular, $\pm$ containing gynostegium; *lobes* with pale cilia along margins. *Corona*; *outer lobes* ascending; *inner lobes* adpressed to backs of anthers then ascending and strongly recurved, dorsiventrally flattened for whole length and sometimes contiguous for some of length, apically obtuse to bifid or even deeply bifid, towards base somewhat dorsally swollen into 2 gibbosities or with 2 horns contiguous with outer corona.

Distribution and habitat

Subsp. *valida* has been found in Namibia in the Caprivi Strip, in Botswana north of the Okavango Delta and eastwards to around Pandamatenga. It has also been collected in western Zimbabwe and southern Zambia.

Plants grow in dry, open forest and are often associated with *Colophospermum mopane* woodland.

Diagnostic features and relationships

Subsp. *valida* has the robust habit and stout, boldly toothed stems of *O. huillensis* subsp. *huillensis* and the plants form large clumps on the surface of the soil. They are not at all rhizomatous.

The maroon to dark purple-red flowers are 35-45 mm across, with narrowly deltate lobes and a cupular tube 5-6 mm deep containing the corona. There are pale, often whitish, vibratile, clavate cilia all along the margins of the lobes.

The corona has steeply ascending outer lobes. The inner lobes are dorsiventrally flattened for their whole length, rising in a column above the centre then broadly spreading towards the apices, which are often quite deeply bifid. In some plants they may be quite tightly

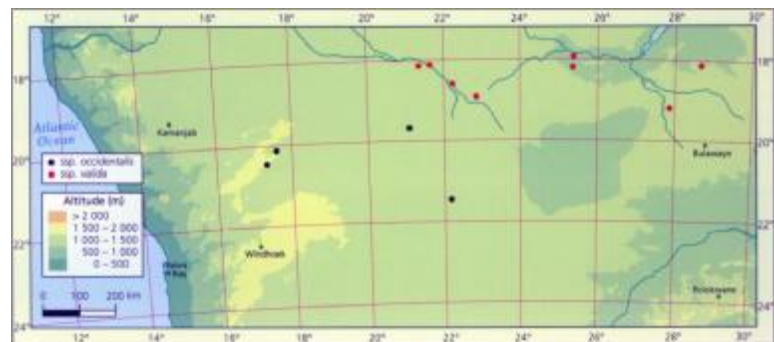
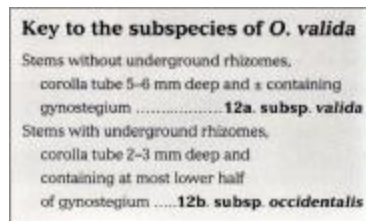


Fig. 10.83. Distribution of *Orbea valida*.

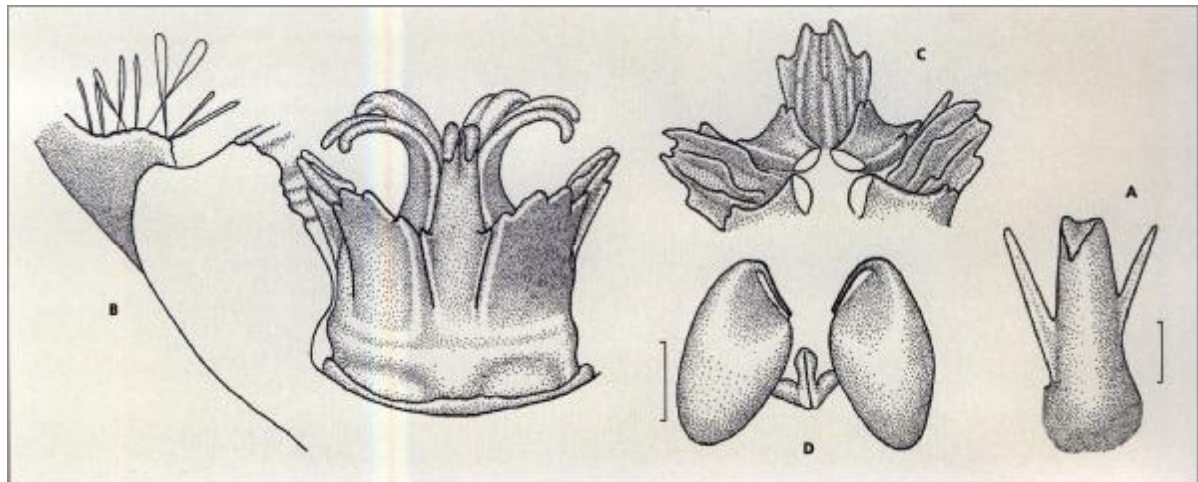


Fig. 10.84. *Orbea valida* subsp. *valida*. A, bract from inflorescence. B, side view of centre of dissected flower. C, face view of part of gynostegium. D, pollinarium. Scale bars: A-C, 1 mm (at A); D, 0.25 mm. Drawn from: PVB 6963, north of Pandamatenga, Botswana.



Fig. 10.85. *O. valida* subsp. *valida*, PVB 6963, north of Pandamatenga, Botswana.

pressed against one another in their lower parts but in others this is not the case. Near the base each lobe is dorsally considerably swollen and this swelling may be somewhat bifid or may take the form of teeth pressed to the side of the outer corona. In such cases there is much reduced access to the guide-rails.

History

Caralluma valida was discovered by Emil Holub, a Czechoslovakian explorer, on one of his two expeditions towards the Zambezi. On both of these expeditions he travelled northwards along the same route (Gunn & Codd 1981) and stayed for extended periods at Pandamatenga

in north-eastern Botswana. Since subsp. *valida* occurs in this area it is possible that he found it in that vicinity either in 1875 or in 1885. The next known record of this subspecies was made in about 1937 by Louis Thompson but it is also unknown where this was collected (Leach 1965). The first specimen for which a definite locality was recorded was one collected by D.C.H. Plowes in the Matopos of western Zimbabwe which flowered in cultivation in 1951. Shortly after this it was collected by L.E. Codd during the Bernard Carp Barotseland Expedition of June-August 1952. This plant was found in Zambia along the Cuando River near the border with Angola.



Fig. 10.86. *O. valida* subsp. *occidentalis*, PVB 6465, north-east of D'Kar, Botswana.

12b. *Orbea valida* subsp. *occidentalis*

Orbea valida subsp. *occidentalis* Bruyns, *Aloe* 37: 76 (2001).

Type: Botswana, north-east of D'Kar, Bruyns 6465 (BOL).

Succulent forming diffuse clumps 80-200 diam. joined by underground rhizomes up to 200 mm long. Stems 40-150 mm long, 15-20 mm thick (excluding teeth), relatively slender; tubercles 5-15 mm long. Corolla 40-45 mm diam.; inside pinkish red; tube 2-3 mm deep, shortly conical, containing at most lower half of gynostegium; lobes with dark red cilia along margins. Corona; outer lobes spreading; inner lobes adpressed to backs of anthers then ascending and recurved, dorsiventrally flattened near base and almost terete towards tips, obtuse, towards base dorsally swollen just above outer lobes into rounded boss.

Distribution and habitat

Subsp. *occidentalis* occurs in Namibia east of the Waterberg from where it continues eastwards into Botswana. Here it has been found near Kangwa and a little north of Ghanzi.

In these areas it grows among *Terminalia sericea*, *Commiphora* and other trees on red to orange sands.

Diagnostic features and relationships

The stems of subsp. *occidentalis* are much more slender than those of subsp. *valida* and they have a strongly rhizomatous habit so that clumps remain comparatively small. Underground rhizomes may spread from their parent plant for up to 200 mm before emerging from the ground.

Here the corolla is pinkish red rather than the usual deeper colour of subsp. *valida* but it also emits an awful smell of old excrement. The tube is much shorter than in subsp. *valida* and the cilia along the margins of the lobes are darkly coloured rather than pale and are scattered all the way along the margins of the lobes.

In subsp. *occidentalis* the corona is much more akin to that of *O. huillensis* than to that of subsp. *valida*. The outer lobes are more spreading and are extremely variable in shape and the inner lobes have the characteristic rounded dorsal boss near the base. The inner corona lobes are broader than usually seen in *O. huillensis* but narrower than in subsp. *valida*. The considerable difference in the shape of the dorsal outgrowths on the inner corona between subsp. *occidentalis* and subsp. *valida* is not considered to be important in view of the extreme variation seen in the one collection of *O. huillensis* subsp. *flava* (fig. 10.78) where some flowers had coronas as in subsp. *valida* and others had them as in subsp. *occidentalis*. The size of the flowers and the many cilia along the margins of the corolla lobes are typical of

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O. valida and consequently these plants have been placed under that species rather than under *O. huillensis*.

History

This subspecies was first noticed in the Waterberg National Park by the conservator Trygve Cooper. My own collections were made independently, first in 1993 east of the Waterberg in Namibia and I collected it for the first time in Botswana in December 1995.



Fig. 10.87. *O. valida* subsp. *occidentalis*, PVB 5529, east of Waterberg, Namibia.



Fig. 10.88. *O. valida* subsp. *occidentalis*, PVB 6465, north-east of D'Kar, Botswana.

13. *Orbea ciliata*

Orbea ciliata (Thunb.) L.C. Leach, *Kirkia* 10: 291 (1975).

Stapelia ciliata Thunb., *Prodr.* 1: 47 (1794).

Podanthes ciliata (Thunb.) Haw., *Syn. Pl. Succ.*: 34 (1812).

Tromotriche ciliata (Thunb.) Sweet, *Hort. Brit.*, ed. 2: 358 (1830).

Diplocyatha ciliata (Thunb.) N.E. Br., *J. Linn. Soc. Bot.* 17: 168 (1878).

Type: South Africa, Cape, between Roggeveld Mountains and Paardeberg, *Thunberg & Masson* 6327 (UPS).

Succulent forming mat 100-500 mm diam., not rhizomatous. Stems 40-80 (-120) mm long, 15-25 mm thick (excluding teeth), stout and often nearly cylindrical, shortly decumbent, green heavily marked with purple-brown to nearly entirely purple-brown; tubercles 5-8 mm long, conical, arranged loosely into 4 very broadly obtuse rows along stem $\pm$ without groove between rows, tapering into spreading conical acute tooth with pair of minute stipular denticles shortly below apex, both apex and denticles obsolescent with age. Inflorescence 1 per stem arising near base $\pm$ without peduncle, of 1 (-2) flowers; pedicel 10-25 mm long, 3-4 mm thick, spreading with ascending apex, holding flower facing upwards close to ground, heavily streaked with purple-brown on green; sepals 6-8 mm long, 3 mm broad at base, ovate-acuminate. Corolla 70-110 mm diam., rotate to shallowly bowl-shaped; outside smooth, pale green dotted and streaked with reddish purple, usually with 5 slightly raised darker

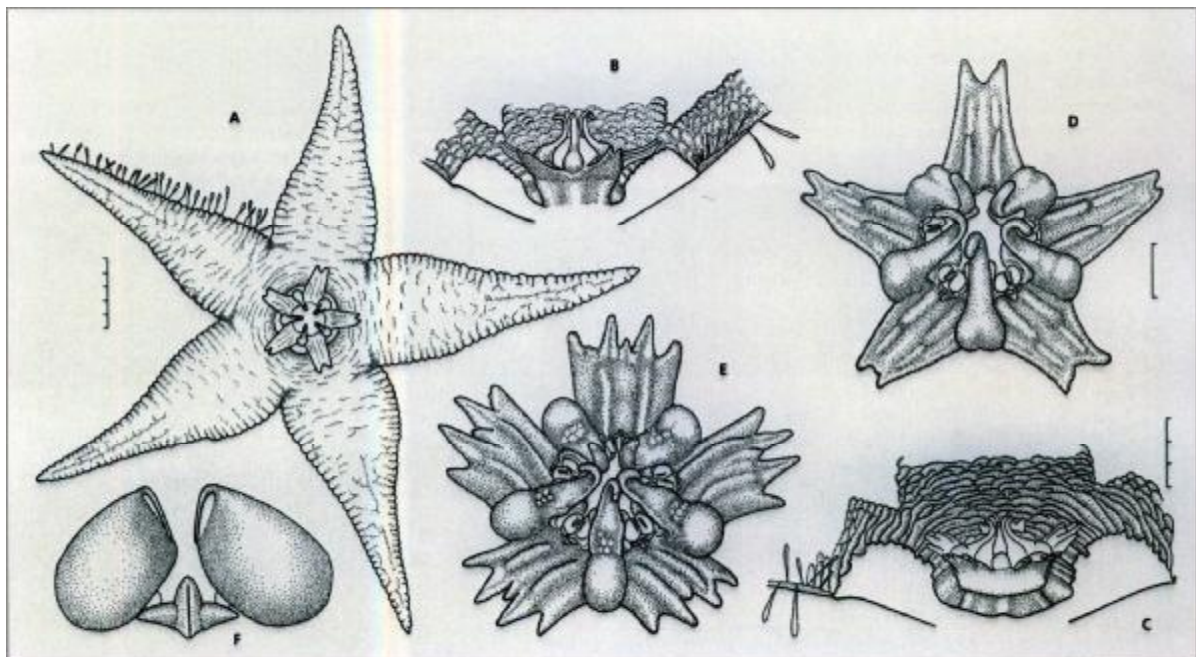


Fig. 10.89. *Orbea valida* subsp. *occidentalis*. A, face view of flower. B, C, side view of centre of dissected flower. D, E, face view of gynostegium. F, pollinarium. Scale bars: A, 5 mm; B, C, 3 mm (at C); D, E, 1 mm (at D); F, 0.25 mm (at C). Drawn from: A, B, D, F, PVB 6465, north-east of D'Kar, Botswana; C, E, PVB 5529, east of Waterberg, Namibia.

veins along lobes; inside cream to pale greenish yellow, covered (more densely towards base) with small papillate $\pm$ transverse ridges, papillae tipped with purple-red; *tube* shallowly bowl-shaped, towards base with broadly funnel-shaped annulus 8-11 mm tall with spreading (to recurved) thickened sometimes slightly pentagonal rim and walls 2-3 mm thick, annulus papillate as inside of corolla but inside more darkly coloured, uniformly dark purple in ring at base around corona and there densely covered with short stiff acute erect purple bristles; *lobes* 28-32 mm long, 14-20 mm broad at base, ovate-deltate, acuminate, spreading to strongly reflexed, with dense row of vibratile clavate white cilia 3-4 mm long along margins. *Corona* $\pm$ 2.5 mm tall, 4.5 mm broad, raised very slightly above base of tube on stout obtusely pentagonal heavily purple-blotched stipe, cream to pale yellow sparsely dotted with purple mainly towards margins; *outer lobes* $\pm$ 0.7-2.0 mm long, 2.0-2.5 mm broad, subquadrate, irregularly obtuse to emarginate or sometimes bidentate, pale yellow sparsely dotted with purple, ascending-spreading, usually pressed against sides of narrow tube formed by base of annulus; *inner lobes* 0.6-1.0 mm long, adpressed to backs of anthers but shorter than them, $\pm$ ovate, acute, somewhat gibbous on rear.

Distribution and habitat

Orbea ciliata is only found in the south-western part of South Africa, where it grows mainly along the eastern boundary of the winter-

rainfall region in several apparently disjunct areas. *Orbea ciliata* is quite common around Calvinia and has often been collected in the vicinity of Karooport in the Ceres Karoo. It has also been recorded much further east at Kruidfontein and around Prince Albert on the southern boundary of the Great Karoo. There is also a single record from Springbok but, as this is somewhat doubtful, it has been left off the distribution map here.

Plants of *O. ciliata* usually grow in flat areas under bushes and they are often associated with spiny species of *Ruschia*.

Diagnostic features and relationships

Orbea ciliata has stout stems which are mostly not more than four times as tall as thick. They are beautifully marked with purple-brown on green, especially if grown in a sunny spot. The stems are ornamented with prominent conical tubercles that taper into a fine, acute tip and are rather vaguely arranged into four rows. These tubercles start off with an acute tip but this soon wears off to leave a rounded greyish scar. The stems of *O. ciliata* are impossible to separate from those of *O. namaquensis*.

Florally these two species are quite different and, with its large, creamy, ciliate flowers with

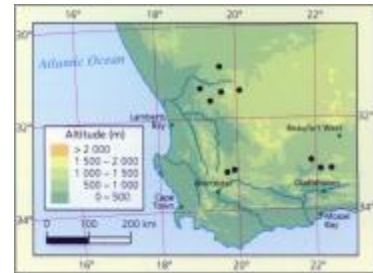


Fig. 10.90. Distribution of *Orbea ciliata*.

particularly prominent annulus, *O. ciliata* is unmistakable. The flowers can be enormous, reaching a diameter of over 100 mm in some plants from around Prince Albert (but they are more usually 70-80 mm in diameter) and they have a most unusual colour for a stapeliad. The inside of the flower, including the annulus, is covered with a fairly dense patchwork of irregular, short ridges which are usually tipped with purple-red. These purple-red patches are only faint towards the bases of the lobes but are more intense on the annulus and also towards the tips of the lobes where they often spread down onto the surface between the ridges. This makes the upper third of the

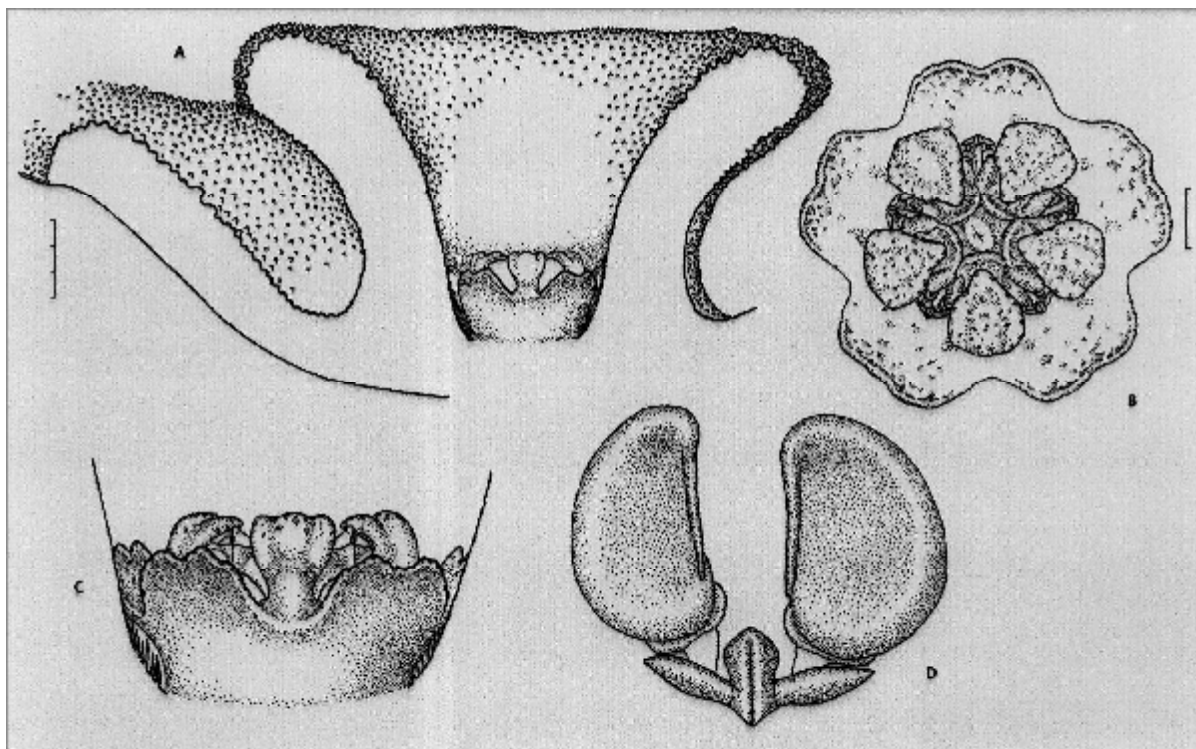


Fig. 10.91. *Orbea ciliata*. A, side view of centre of dissected flower. B, face view of gynostegium. C, side view of gynostegium. D, pollinarium. Scale bars: A, 3 mm; B, C, 1 mm (at B); D, 0.25 mm (at A). Drawn from: PVB 4332, north-west of Calvinia.

ORBEA CILIATA

lobe darker in colour than towards the centre. The background colour of the flower is cream to faintly greenish yellow with a generally more intense cream on the annulus. The only relief from the general cream colour comes in the base of the tube behind the corona where it is dark purple. Here there is also a dense ring of small, thick bristles (fig. 29 H). The only other hairs present on the flower are those that make up the dense fringe of white, slightly clavate, vibratile cilia along the margins of the lobes. These are present along almost the whole length of the lobes (except around the last 2-4 mm near the tip) and move en masse in the slightest stirring of air.

Probably the most unusual feature of the flower is the remarkably prominent annulus. The corolla itself is bowl-shaped, with spreading, often slightly recurved lobes. Near the base of this bowl there is another thick funnel-shaped, corolla-like structure that is usually nearly as tall as the corolla tube is deep. This structure is a much enlarged annulus, the largest annulus found in any stapeliad. Towards its base it becomes narrow and the relatively small corona fits closely into it, with the outer lobes

pressed against its sides.

In colouring the corona matches the corolla closely. It is cream with purple-brown spots, particularly on the edges of the outer lobes and all over the inner lobes (apart from a very dark patch near the base of each inner lobe and a paler patch on each outer lobe beneath the guide-rail). Both the outer and the inner lobes are short and simple, with the outer lobes almost rectangular and forming a deeply indented, pentagonal platform below the inner and the inner lobes adpressed to but not covering the anthers.

History

Orbea ciliata was discovered by Carl Pehr Thunberg and Francis Masson in November or December 1774 during Masson's first stay in the Cape. They found it in the southern part of the Ceres Karoo and the painting of it in Masson's *Stapeliae Novae* was made in habitat on this occasion. After then it seems to have been lost for a long time until it was rediscovered by Rudolf Marloth in 1905 near Prince Albert (Marloth 1932). The plants that Marloth

sent to N.E. Brown at Kew caused the latter much excitement, as he had never expected to see this beautiful species in the living state (Brown 1907-09).

Thunberg described this species as *Stapelia ciliata* and it was moved to *Podanthes* by Haworth and to *Tromotriche* by Sweet. In 1878 N.E. Brown erected a monotypic genus, *Diplocyatha*, for it, mainly because of the large, tubular process (the annulus) arising from the base of the corolla tube. Thunberg mistook this structure for the outer corona but today it is recognised as a much modified annulus and is the most extreme example of such an annular swelling found among the stapeliads.



Fig. 10.92. *O. ciliata*, PVB 4332, north-west of Calvinia.



Fig. 10.93. *O. ciliata*, PVB 3694, east of Prince Albert, an exceptionally large flower about 110 mm in diameter.

ORBEA HALIPEDICOLA

14. *Orbea halipedicola*

Orbea halipedicola L.C. Leach, *Exceisa* Taxon. Ser. 1: 40 (1978).

Stapelia halipedicola (L.C. Leach) P.V. Heath, *Calyx* 1: 16 (1992).

Type: Moçambique, between Buzi and Gorongosa Rivers, *Ambrose sub Leach* 12396 (SRGH, holo PRE, LISC, iso.).

Orbea halipedicola subsp. *septentrionalis* L.C. Leach *Exceisa* Taxon. Ser. 1: 43 (1978).

Stapelia halipedicola var. *borealis* P.V. Heath, *Calyx* 1: 16 (1992).

Type: Moçambique, Gorongosa Park, 14/5/1972, Tinley (SRGH).

Small succulent forming diffuse clump up to 2 m diam., often rhizomatous. Stems 50-150 mm long, 4-7 mm thick (excluding teeth), slender, usually decumbent, green and often streaked with brown; tubercles 7-12 mm long, arranged into 4 obtuse rows along stem, tapering into slender conical-acute ascending to slightly incurved tooth flattened above near apex, with pair of short ascending denticles 2-3 mm below apex. Inflorescence 1 per stem near base, of 1-3 flowers developing in gradual succession on peduncle < 5 mm long, with few tiny bracts up to 2 mm long; pedicel 20-30 mm long, $\pm$ 2 mm thick, spreading with upturned apex so flower facing upwards near ground; sepals 4-6 mm long, 2.0-2.5 mm broad at base, narrowly ovate, acuminate. Corolla 30-42 mm diam., rotate; outside pale creamy green, smooth and obscurely 3-5-nerved; inside with small acute papillae especially towards apex of lobes and on annulus, otherwise smooth and not rugulose, deep red to red- or purple-brown with irregular yellow to whitish markings; tube formed by $\pm$ circular

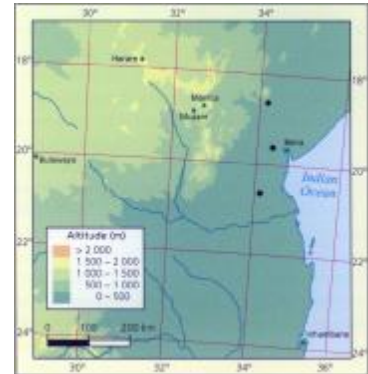


Fig. 10.94. Distribution of *Orbea halipedicola*.

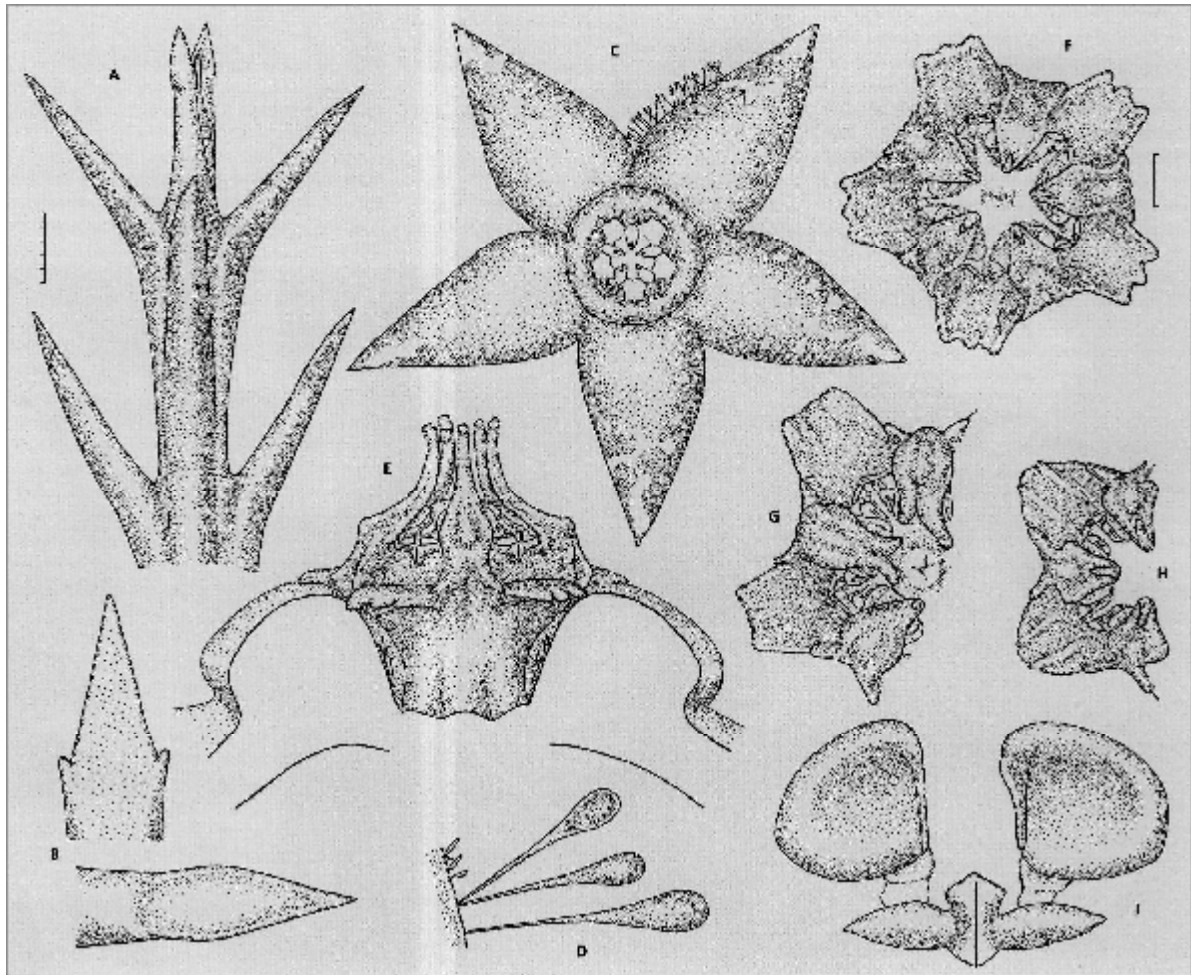


Fig. 10.95. *Orbea halipedicola*. A, apex of stem. B, apex of tubercle. C, face view of flower. D, cilia along margins of lobes with tiny ones sometimes present near bases of lobes. E, side view of centre of dissected flower. F-H, face view of gynostegium (or part). I, pollinarium. Scale bars: A, C, 5 mm (at A); B, 1 mm (at A); D, 0.5 mm (at A); E-H, 1 mm (at F); I, 0.25 mm (at A). Drawn from: A, B (lower one), H, PVB 7401, south of Tico, Sofala Province, Mocambique; rest, PVB 7402, north of Save River, Sofala Province, Mocambique.

ORBEA HALIPEDICOLA

and slightly to strongly convex annulus 1.5-2.5 mm tall and 8-9 mm broad with spreading obtuse and sometimes slightly recurved margin; lobes 14-16 mm long, 7-10 mm broad at base, spreading, ovate, shortly acuminate, convex above especially towards base from downwardly folded margins, with vibratile clavate (later spatulate) white to purple-red marginal cilia 1-2 mm long in lower half. Corona 5 mm tall, 5.0-6.5 mm diam., raised on stout slightly pentagonal stipe nearly 2 mm long; *outer lobes* ± 2 mm long, 1.5 mm broad, spreading, slightly recurved to rest on rim of annulus, $\pm$ subquadrate, often thickened along middle and sometimes with 2 raised radial ridges forming central trough produced into fleshy tooth, truncate and irregularly dentate, dark purple-brown; *inner lobes* 3-4 mm long, ± 1 mm broad, adpressed to backs of anthers, becoming erect and sometimes connivent above, dorsiventrally flattened narrowing to terete above with slightly clavate and obscurely rugulose apex, dorsally gibbous and produced towards base into pair of subacute fleshy teeth laterally fused to outer lobes, bright yellow spotted with red or purple.

Distribution and habitat

Orbea halipedicola is known only from central Moçambique. Here it is recorded in a few places in the coastal flats north of the Save River and north of the Buzi River. Records have also been made in the former Gorongosa Park, to the north-east of Beira.



Fig. 10.96. *O. halipedicola*, PVB 7401, south of Tico, Sofala Province, Mocambique.



Fig. 10.98. *O. halipedicola*, PVB 7401, south of Tico, Sofala Province, Mocambique, with a particularly swollen annulus.



Fig. 10.97. *O. halipedicola*, PVB 7401. The annulus often has a yellow ring on its edge as here.



Fig. 10.99. *O. halipedicola*, PVB 7402, north of Save River, Sofala Province, Mocambique.

Plants grow in a variety of habitats. They were recorded growing in *Colophospermum mopane* woodland in the Gorongosa Park

(Leach 1978a) and are very common in a few spots in the low-lying flats south-west of Beira. The two localities known to me in this area (one



Fig. 10.100. *O. halipedicola*, PVB 7401, south of Tico, Sofala Province, Mocambique.

shown in fig. 50) are characterised by firm, white, finely gravelly and somewhat calcareous sand of almost neutral pH. This forms open, almost completely bare patches that are sometimes inundated by fresh water. These open patches surround slightly raised clumps of bushes and trees in which the small palm *Hyphaene natalensis* and a species of *Strychnos* are particularly common. It is around the edges of these clumps of vegetation, usually among fine grasses, with a species of *Portulaca* and often with low-growing specimens of *Adenium obesum* that *O. halipedicola* is found.

Diagnostic features and relationships

Plants of *O. halipedicola* spread very extensively underground with rhizomes, forming diffuse clumps up to 2 m in diameter and often with only single erect stems projecting from the soil over much of this area. The stems are slender, up to 80 mm tall, erect or spreading (depending very much on the amount of shelter received), usually bright green and sometimes mottled with brown. Like several of the tropical orbeas, they have long, slender, ascending tubercles which break up their outline and make them harder to see among tufts of grass. Flowers are borne in gradual succession near the bases of the younger stems. The pedicels usually spread away from the stems but have an upturned apex so that the flower faces upwards, often flat on the ground but sometimes above it. The very strikingly coloured flowers are around 40 mm in diameter and almost completely flat. They remain open for up to nine days and give off a bad odour of rotten fish or rotten meat for most of this time. Very variable in colour, they are variously transversely striped and mottled with cream to yellow on red to purple-brown. Many of them are almost wholly deep red with a few bright yellow markings near the tips of the lobes. In others yellow markings may be present, sometimes quite densely and very brightly over the whole of the surface so that the flower is more yellow than red. In the centre there is a low but conspicuous annulus which forms the corolla tube and is slightly undercut around its edges. On the annulus the background dark colour is the same as the rest of the flower but the yellow markings are noticeably paler and usually form one or more rings, one of which often lies just at the edge of the annulus, more or less outlining it. The lobes usually have their margins folded back and lined with white to purple-red cilia which are clavate at first and later dry out to become spatulate. There are often other, much smaller, thickened papillae near the bases of the lobes.

The corona in the centre has short, nearly rectangular outer lobes spreading on the annulus at the mouth of the tube and inner lobes

rising in the centre with very slightly thickened apices. The outer lobes often have two parallel ridges forming a channel along their middle but this can be absent and the upper surface is then almost flat. They are usually darker than the red or purple of the corolla but the inner lobes are yellow with fine reddish spots, matching the yellow markings on the corolla.

Orbea halipedicola is similar to *O. umbracula* and *O. woodii* in many respects. All of them have slender tubercles on the stems. In *O. umbracula* the flowers are held on an erect pedicel while in the other two species the pedicel spreads outwards and the flowers are often pressed to the ground. In all of them the annulus gives rise to the corolla tube and it is broadest and flattest in *O. halipedicola*, where the corolla lobes are also the least reflexed and are not at all transversely rugulose. The same short, broad outer corona lobes, often with a channel down the middle, are found in all three and the respective coronas only differ somewhat in the nature of the tips of the inner lobes. These do not extend beyond the anthers in *O. woodii* but do extend beyond the anthers and rise up in the other two, to the greatest extent in *O. umbracula*, where they are noticeably swollen and tuberculate at the tips. There is also a relationship with *Orbea semota* from further north in Kenya and Tanzania, but this has a more rugulose corolla with an even flatter annulus than in *O. halipedicola* and its stems more closely resemble those of *O. variegata*.

Leach recognised two subspecies: subsp. *septentrionalis* recorded from the Gorongosa Park and from near Beira, and the typical subspecies from between the Buzi and Gorongosa rivers a little south of this. Subsp. *septentrionalis* was distinguished by erect, thicker stems with shorter teeth, a less distinctly raised annulus and almost flat outer corona lobes. However, plants indistinguishable from subsp. *halipedicola* have been found near Beira [PVB 7401], among other specimens characteristic of subsp. *septentrionalis*. It seems, therefore, that the characteristics of subsp. *septentrionalis* fall within the range of variation of the species within some of its populations and so it is not recognised here.

History

Orbea halipedicola seems to have been discovered by Mrs. Jean Ambrose (25 February 1915-) in about 1960. She brought material to L.C. Leach who also found it in two localities during his investigations into the succulent species of *Euphorbia* in Moçambique. During his ecological surveys of the former Gorongosa Park conducted during the 1970s, Kenneth L. Tinley observed it in several places in the park. Until recently these were the only records for the species.

15. *Orbea woodii*

Orbea woodii (N.E. Br.) L.C. Leach, *Kirkia* 10: 290

(1975). *Stapelia woodii* N.E. Br., *Gard. Chron. Ser. 3*, 11: 554

(1892). Type: South Africa, Natal, Noodsberg, Medley

Wood 4119 (K).

Orbea woodii var. *westii* R.A. Dyer, *Fl. Pl. South Africa*

21: t. 811 (1941). Type: Natal, Estcourt, West 1531 sub PRE

26437

(PRE).

Dwarf succulent forming diffuse clump up to 300 mm diam., not rhizomatous. Stems 40-60 mm long, 6-8 mm thick (excluding teeth), branching from base, erect to shortly decumbent, green mottled with purple-brown; tubercles 6-15 mm long, arranged loosely into 4 obtuse rows along stem ± with groove between rows, tapering into prominent slender conical-acute ascending-spreading tooth often with pair of small denticles shortly below apex. Inflorescence 1 per stem near base, of 1-6 flowers developing successively occasionally on stout peduncle < 5 mm long; pedicel 20-55 mm long, 1.5-2.5 mm thick, spreading horizontally with upturned apex; sepals 5.5-7.0 mm long, 1.5-2.0 mm broad at base, narrowly ovate-acuminate. Corolla 30-45 mm diam., rotate to slightly reflexed; inside red-brown to deep maroon-brown, rarely faintly transversely barred with yellow; tube ±1.5 mm deep, conical, formed entirely by thick cushion-like to ± dome-shaped smooth to slightly rugulose annulus often slightly darker than or paler than lobes; lobes 12-18 mm long, 6-10 mm broad at base, spreading to somewhat reflexed, ovate and shortly acuminate to narrowly ovate-acuminate, convex with margins sometimes quite strongly recurved, lightly to heavily transversely rugulose, very finely papillate, with clavate vibratile marginal cilia up to 2 mm long. Corona ± 4.5 mm tall, 4.5-7.0 mm broad, darker than annulus to almost black, raised on short stout obtusely pentagonal stipe ± 1 mm long; outer lobes 1.5-2.0 mm long, 1.0-1.5 mm broad, more or less truncate and obtusely dentate or crenulate at apex, with 2 raised fleshy ridges forming trough running down centre, resting on annulus; inner lobes 1.2-2.0 mm long, adpressed to backs of anthers.

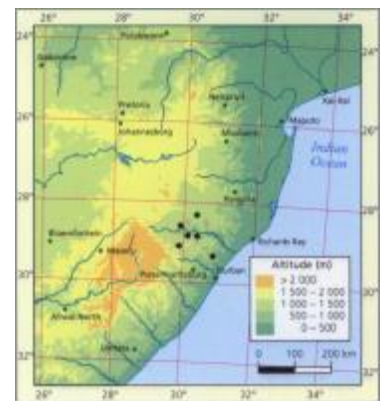


Fig. 10.101. Distribution of *Orbea woodii*.



Fig. 10.102. *O. woodii*, PVB 9334, near Weenen, flower with uniform colour and especially tall and smooth annulus.

sometimes exceeding them then shortly connivent-erect in centre, dorsiventrally flattened and broadly ovate below, acuminate, margins sometimes slightly raised (then lobes channelled above) and occasionally with 1-2 small obtuse teeth, sometimes with small dorsal tubercle.

Distribution and habitat

Orbea woodii is known only in central KwaZulu-Natal along the middle reaches of the Tugela River valley in the area between Dundee, Ladysmith, Estcourt and Kranskop. Very few records have been made in the past 30 years. Plants of *O. woodii* grow on gently sloping



Fig. 10.103. *O. woodii*, PVB 9334, near Weenen, flower with faintly rugulose but well-defined annulus.

areas of shale with scattered dolerite rocks, where they are found between stones and small tufts of grass in open places among scattered trees of *Acacia tortilis* and *A. karroo*. Although *Aloe marlothii* and a few small succulents grow with it, *O. woodii* has not been observed in the highly succulent *Aloe* and *Euphorbia* scrub of the Mooi River and Tugela River valleys and may not occur there at all. It was interesting that, where it was seen in December 2002 near Weenen, the stems of *O. woodii* were grazed off towards the tips but that this had not befallen either *O. lutea* or *Duvalia polita*, with which it was growing.

Diagnostic features and relationships

The stems of *O. woodii* have relatively long tubercles tapering to a slender tooth. As such they resemble somewhat those of *O. longidens* but they are not quite as slender and have a generally darker green colour with a more intense mottling of purple-brown.

However, the flowers are markedly different. In *O. woodii* they are borne on slender, spreading pedicels and are various shades of brown, mostly without any spots or other markings. The lobes are usually somewhat reflexed, pushing the centre of the flower forwards and they often have strongly reflexed margins so they are convex and can be fairly narrow. Their surface is generally densely and finely rugulose. In the centre there is a swollen, usually smooth annulus, which is made more prominent by the manner in which the lobes are somewhat reflexed and by the fact that it may be slightly differently coloured to the rest of the flower. It forms a small corolla tube surrounding the base of the gynostegium in the otherwise more or less flat centre of the flower. The outer corona lobes are fairly short, with radial ridges defining a central area on each

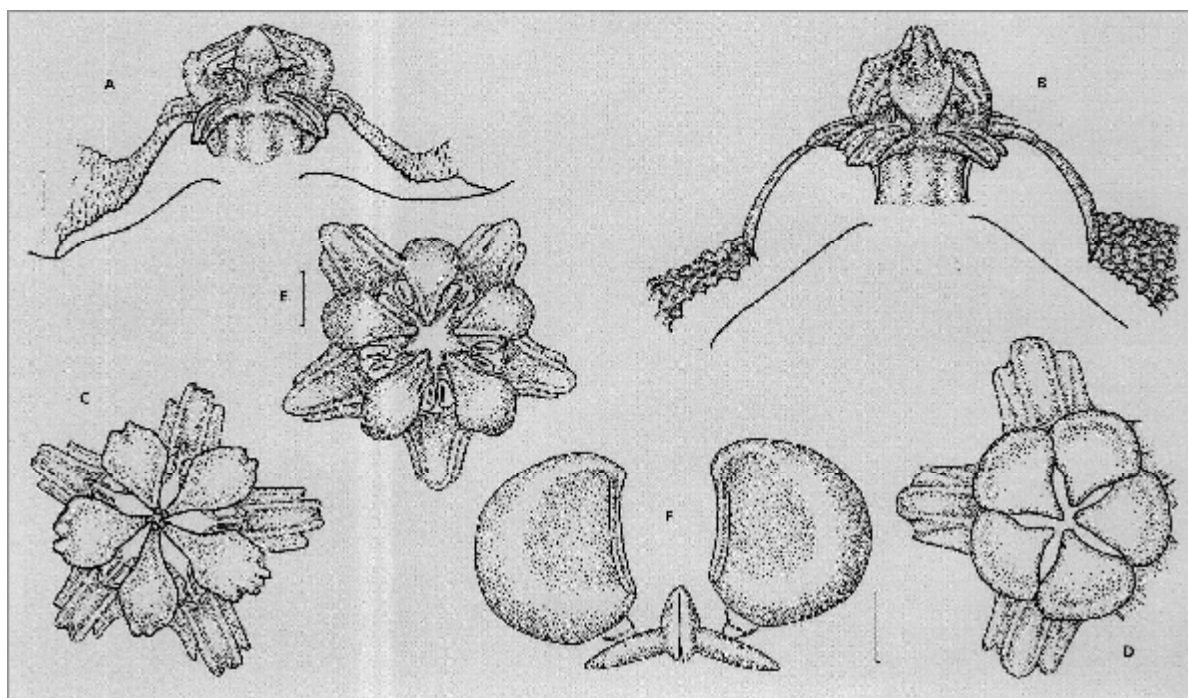


Fig. 10.104. *Orbea woodii*. A, B, side view of dissected flower showing variation in thickness of the annulus around the mouth of the tiny corolla tube and the length of the inner corona lobes. C-E, face view of gynostegium, showing variation in the breadth of the inner corona lobes. F, pollinarium. Scale bars: A, B, 2 mm (at A); C-E, 1 mm (at E); F, 0.25 mm. Drawn from: A-D, Bruyns 9334, near Weenen; E, F, Frandsen, 8-9 miles south-east of Helpmekaar.



Fig. 10.105. *O. woodii*, PVB 9334, near Weenen, unusually darkly coloured flower with faint transverse yellowish markings and only slightly raised, obscure annulus.

lobe which is slightly longer than the rest of the lobe. The inner lobes are variable in length and may exceed the anthers and even, in some cases, rise a short distance in the centre.

Orbea woodii shares many features with *O. halipedicola*, *O. semota* and *O. umbracula* and, of these, it is most similar to *O. halipedicola* from Mozambique and *O. semota* from East Africa. In *O. halipedicola* the stems are somewhat different and the inside of the flower is not at all rugulose, while the inner corona lobes are markedly longer than those of *O. woodii*. The stems of *O. semota* are similar to those of *O. woodii*. The inside of the corolla in *O. semota* is also rugulose (as in *O. woodii*) and the annulus may be finely rugulose or smooth. However, it is much broader and flatter than that of

O. woodii and in *O. semota* the gynostegium is raised on a considerably shorter stipe. Leach (1978a) also mentioned that the inner corona lobes of *O. semota* were quite different from those of *O. woodii* in that they were 'usually truncate or dentate at the apex'. However, they have also been found to be acute in some plants of *O. semota* so this does not always prove to be useful.

History

Orbea woodii was discovered by John Medley Wood on the Noodsberg, which lies in the mountainous country along the Tugela River to the west of Stanger. He sent material to Kew which flowered in May 1890.



Fig. 10.106. *O. woodii*, PVB 9334, near Weenen, at the base of a small dolerite rock, with short grasses and with tips of the stems slightly grazed off, December 2002.

16. *Orbea maccloughlinii*

Orbea maccloughlinii (L.Verd.) L.C.Leach, *Kirkia* 10: 291 (1975).

Stapelia maccloughlinii L.Verd., *Fl. Pl. South Africa* 21: t 812 (1941).

Type: Cape, Transkei, Umtata Falls, McLoughlin sub PRE 26384 (PRE).

Orbea speciosa L.C.Leach, *Excelsa Taxon. Ser.* 1: 33 (1978).

Stapelia speciosa (L.C.Leach) P.V.Heath, *Calyx* 1: 16 (1992).

Type: South Africa, Natal, Izingsolweni, Lubbers sub Leach 14742 (PRE).

Orbea doldii Plowes, *Asklepios* 86: 9 (2002).

Type: South Africa, Eastern Cape, Buntingville, Dold 4455 (GRA).

Dwarf succulent forming small clump, sometimes extensively rhizomatous. Stems 30-100 mm long, 6-8 mm thick (excluding teeth), sometimes forming rhizomes up to 150 mm long, slender, erect to shortly decumbent, pale green flecked with purple-brown; tubercles 4-10 mm long, arranged into 4 obtuse rows along stem with slight groove between rows, tapering into slender spreading conical tooth, with pair of much reduced to obsolescent stipular denticles shortly below apex. Inflorescence 1 per stem near base, of 1-3 flowers developing in gradual succession, with few concave narrowly ovate acute bracts 2-3 (-6) mm long and 1.5 mm broad at base; pedicel (15-) 20-25 mm long, 2 mm thick, heavily streaked with purple-brown on green, ± horizontally spreading often with upturned apex, holding flowers facing horizontally or upwards; sepals 5-12 mm long, 2-3 mm broad at base, narrowly ovate, acute or acuminate. Corolla 35-55 mm diam., rotate to somewhat reflexed right from centre, usually with lobes slightly reflexed; outside glabrous, pale green suffused with purple-brown, with 3-5 longitudinal purple-brown veins along each lobe; inside smooth and somewhat shiny, dark maroon to brown-red with few too many irregular transverse yellow markings towards tips of lobes or with maroon spots on yellow background; tube 2.0-2.5 mm long, ± 5 mm broad, cupular, bounded by annulus that is abruptly to gradually raised 1.5-2.0 mm above surface

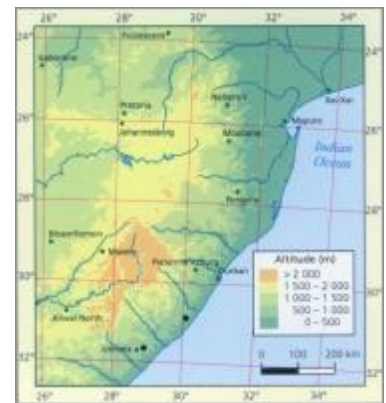


Fig. 10.107. Distribution of *Orbea maccloughlinii*.

ORBEA MACLOUGHLINII



Fig. 10.108. *O. macloughlinii*, collector unknown, Tsitsa Falls in the former Transkei.



Fig. 10.109. *O. macloughlinii*, PVB 8920, near Umtata.

of corolla and abruptly to gradually merging with rest of surface, pentagonal; lobes 12.5-20.0 mm long, 9.0-13.5 mm broad at base, spreading and often reflexed, ovate-deltate, shortly acuminate, rarely slightly rugulose towards tips, margins not folded back, with clavate vibratile maroon marginal cilia up to 3 mm long except at tips. Corona $\pm$ 4 mm tall, 6.5-7.0 mm broad, raised well above base of tube on dark maroon obtusely pentagonal stipe $\pm$ 1.5 mm long and 2.5 mm thick; outer lobes $\pm$ 1.5-2.0 mm long, 1.5-2.0 mm broad, subquadrate, spreading and touching upper rim of annulus, truncate to obtusely 3-4-dentate, emarginate, dark maroon; inner lobes 1-2 mm long, adpressed to backs of anthers and shorter than to slightly exceeding them, $\pm$ ovate, acute to truncate, slightly gibbous on rear, irregularly and sparingly dentate on margins, yellow minutely speckled with red.

Distribution and habitat

Orbea macloughlinii is only known from the former Transkei in the Eastern Cape and from a single locality in southern KwaZulu-Natal, in the sandstone hills at the Oribi Gorge near Izingolweni. In the former Transkei it has been collected along the Umtata River at the Umtata Falls which were just east of Umtata and, reputedly, near the Tsitsa Falls some 60 km to the north of Umtata.

Plants of *O. macloughlinii* grow in dry places in shallow soils along the precipitous edges of river banks or in areas where slabs of dolerite bedrock are close to the surface. In such places the rock surfaces become hot during the day.

Although the rainfall is relatively high (500-700mm annually) and the rocks will sometimes be seen to be streaming with runoff water, these habitats are periodically quite arid. Consequently they are often colonised by a selection of succulents such as *Anacampseros rufescens*, species of *Crassula* and *Delosperma*, and various geophytes such as *Brachystelma cafferum*.

Diagnostic features and relationships

The stems of *O. macloughlinii* form loose clumps and have a very similar shape to those of *O. verrucosa*, except for a distinctly rhizomatous habit in some plants. They look somewhat different from the stems of *O. longidens* as the tubercles are not nearly as long and are more abruptly acute.

The flowers are very variable in colour, with a similar variation to that found in *O. halipedicola*, *O. longidens* and *O. semota*. In some the inside has maroon spots on a yellow background. The spots become finer towards the centre where the yellow is then brightest and they become larger towards the tips of the lobes where they coalesce into a maroon patch. In others the background colour is maroon to brown-red and this is transversely mottled with yellow (sometimes quite sparsely), mainly around the bases of the lobes. They emit a faint

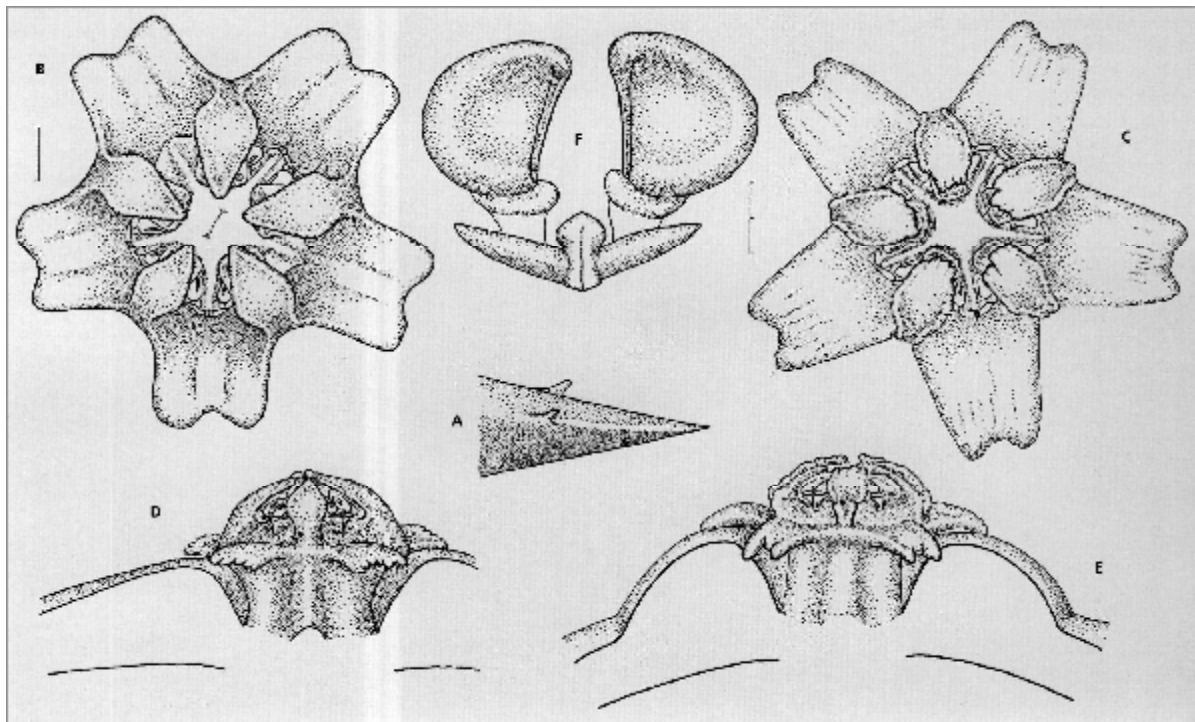


Fig. 10.110. *Orbea macloughlinii*. A, apex of tubercle. B, C, face view of gynostegium. D, E, side view of centre of dissected flower. F, pollinarium. Scale bars: A, 1 mm (at F); B, C, 1 mm (at B); D, E, 2 mm (at F); F, 0.25 mm. Drawn from: A, B, D, F, collector unknown, Tsitsa Falls; C, E, Bruyns 8920, near Umtata.



Fig. 10.111. *O. macloughlinii*, PVB 8920, near Umtata, more brightly coloured than fig. 10.109.

unpleasant odour.

Towards the centre of the flower there is a very variably prominent annulus. In some plants the corolla gradually becomes thicker towards the centre, where there is then a low and barely distinguishable annulus, while in others the annulus is abruptly raised out of the surface near the centre. The annulus is usually about 2 mm tall and may have a distinctly pentagonal outline. It gives rise to a small tube around the gynostegial stipe, beyond which the corolla is either flat or slightly reflexed.

In *O. macloughlinii* the gynostegium is



Fig. 10.112. *O. macloughlinii*, Lubbers sub Leach 14742, near Izingolweni (clonotype of *O. speciosa*), with very brightly coloured flowers indeed.

supported on a stipe which is hidden within the tubelet formed by the annulus. It has comparatively large outer corona lobes which are somewhat rectangular and spread out on the annulus. As in *O. longidens* they have a flap beneath the guide-rail which hides a nectarial cavity alongside the ovaries. Their dark maroon colour in some plants matches the colour of the corolla quite closely but in others they are darker than the corolla. Small droplets of nectar are secreted on their upper surface. The inner lobes are adpressed to the backs of the anthers and may slightly exceed them. They are

yellow with maroon spots and sometimes have a maroon margin.

Orbea speciosa is included within the present concept of *O. macloughlinii*. Previously Leach (1978) thought there were a few floral differences between them. These differences were essentially the almost uniformly dark maroon flower of *O. macloughlinii* with hardly any yellow on it (in *O. speciosa* the corolla was boldly mottled with maroon on yellow inside) and the manner in which, in *O. macloughlinii*, the corolla gradually becomes thicker towards the centre, giving rise to a low annulus which



Fig. 10.113. *O. macloughlinii*, PVB 8920, near Umtata, rhizomatous plants among stones and seeping water on dolerite outcrop, December 2001.

ORBEA LONGIDENS

itself gives rise to a small tube around the gynostegial stipe. In *O. speciosa* the annulus is abruptly raised in the centre of the corolla. There is no discernible difference between the respective coronas. However, Leach was only familiar with a single plant of *O. speciosa* and a single collection of *O. maccloughlinii*. The collection PVB 8920, made within 5 km of the type locality of *O. maccloughlinii* (and at the type locality for *O. doidii*), has shown that these differences do not exist. Here in some plants the corolla is much more brightly and strikingly mottled with yellow on maroon to brown-red than is supposed to be typical for *O. maccloughlinii*, while in others it has the maroon colour with small yellow markings that was described for *O. maccloughlinii*. In some plants of this collection (fig. 10.110 E) the annulus is abruptly raised in the centre of the flower, exactly as in *O. speciosa*, while in others it is considerably less prominent. Consequently *O. speciosa* has been reduced to synonymy and the recently described *O. doidii* is also considered to fall within the range of variation of *O. maccloughlinii*.

History

Orbea maccloughlinii was discovered at the beginning of or just before 1939 by Alfred G. McLoughlin, who was qualified as a lawyer and for 10 years (1936-1946) was the president of the Native Appeals Court in the Transkei. He took a keen interest in science generally and especially in botany and made several of the few known records of succulents in the Transkei (Gunn & Codd 1981).

The Umtata Falls, where this species is said to have been discovered, now lie under a dam. A second collection exists in cultivation from along the Tsitsa River but it is not known when or by whom this was made. Recently a small but prolific locality for this species was discovered near Umtata by Anthony P. Dold, while collecting material for his research on the genus *Bergeranthus* (Aizoaceae) and this was described as *O. doidii*.

Orbea speciosa was discovered by Georg Elfried Kurt 'George' Lubbers (26 March 1912-17 March 1999). Lubbers was a motor mechanic who owned a garage in Johannesburg and had a very keen interest in plants generally and succulents in particular. He was also the discoverer of *Anacampseros subnuda* subsp. *lubbersii*. *Orbea speciosa* was found during an Operation Wildflower expedition to rescue plants from a dam-building operation and it appears to have been in cultivation at least since 1971. All the material of *O. speciosa* in cultivation seems to belong to a single clone and it is very likely that only one plant was ever found. This clone is self-fertile, which is rare among the stapeliads. It is also very easily grown and propagated vegetatively so that it is still quite widespread in collections.

17. *Orbea longidens*

Orbea longidens (N.E. Br.) L.C. Leach, *Kirkia* 10: 290 (1975).

Stapelia longidens N.E. Br., *Gard. Chron. Ser. 3*, 18: 324 (1895).

Type: Mozambique, Delagoa Bay, Monteiro, cult. Tillett (K).

Dwarf succulent forming diffuse clump up to 100 mm diam., sometimes rhizomatous. Stems 50-120 mm long, $\pm$ 5 mm thick (excluding teeth), slender, erect to decumbent, pale green marked with purple-brown; tubercles 5-20 mm long, arranged loosely into 4 obtuse rows along stem with shallow groove between rows, tapering into long slender conical usually ascending tooth mostly with pair of acute denticles inserted about two thirds of distance towards apex. Inflorescence 1 per stem near base, of 1-3 flowers developing in gradual succession on peduncle < 5 mm long; pedicel $\pm$ 20 mm long, spreading sometimes with ascending apex; sepals 6-8 mm long, 1.5-3.0 mm broad at base, ovate-acuminate. Corolla 30-50 mm diam., rotate, deeply lobed; outside pale green, glabrous; inside glabrous and smooth or minutely pubescent towards tips of lobes, cream-coloured or yellowish with numerous small maroon to purple-brown spots within tube which become larger and usually confluent towards apex of lobes; tube $\pm$ 5 mm long, 6-10 mm broad, broadly campanulate but steep-sided, with abruptly raised annulus near base 2-3 mm long and 4-6 mm broad (about 1 mm thick) around base of gynostegium, pentagonal; lobes $\pm$ 16-20 mm long, 6-12 mm broad at base, spreading to reflexed, ovate to ovate-lanceolate, acute, with spatulate cilia 2-4 mm long along margins usually at least in lower half to eciliate, margins often somewhat folded upwards. Corona 3-6 mm tall, 4-5 mm broad, seated on stout pentagonal stipe 2-3 mm long; outer lobes 12-15 mm long, subquadrate, spreading with apices closely recurved over rim of annulus, cream with broad purple-brown patch down middle; inner lobes 12-15 mm long, adpressed to backs



Fig. 10.114. Distribution of *Orbea longidens*.

of anthers, hiding and exceeding them to meet in centre but not produced above them, $\pm$ ovate, acute, slightly gibbous on rear, cream finely spotted with pale purple.

Distribution and habitat

Orbea longidens is known in the southern part of Mozambique from about 90 km north of Maputo southwards to near Catuane. In South Africa it has been recorded in northern KwaZulu-Natal from near Ndumu southwards to around Hluhluwe. Over all of its range, it occurs within 50 km of the coast and at altitudes of 10-100 m.

Plants of *O. longidens* usually grow in flat areas in soft, white or greyish sand among short grasses (fig. 10.120) and are sometimes associated with bushes of *Helichrysum* (around Hluhluwe) or scattered small trees of *Euclea*,



Fig. 10.115. *O. longidens*, PVB 4464, near Mansengwenya.

Strychnos and *Hyphaene natalensis* (north of Maputo). Although many plants were seen in January 1991 around Hluhluwe, this species is mostly not very common and appears to be very rare indeed now around Maputo.

Diagnostic features and relationships

The stems of *O. longidens* sometimes spread underground with horizontal runners but in most cases the plants are entirely superficial, forming small clumps.

Orbea longidens is another of the species of *Orbea* with relatively long tubercles on the stems which give the plants a grass-like appearance

and they can be difficult to spot among tufts of grass, especially once this becomes longer. Here the stems are pale green mottled with purple-brown, with ascending, slender tubercles with a pair of small, stipular denticles near their apex.

The flowers of *O. longidens* are some of the most striking in the genus. They are fairly large and usually brightly coloured with a background of cream spotted with maroon or brown. These spots are usually finest and most sparse towards the centre and tend to increase in size, particularly beyond the middle of the lobes, usually coalescing into a solid, dark patch towards the tips of the lobes. The flower gives off an odour somewhat reminiscent of baboon dung.

In the centre of the corolla there is always a small, steep-sided, usually roughly pentagonal depression which contains the unusually shaped annulus and the corona. Beyond this the corolla may be flat or it may have the lobes quite strongly reflexed. Concealed within the small tube in the centre of the corolla there is one of the most peculiar annuli to be found in *Orbea*. This consists of a thin ridge of tissue which rises abruptly from the flattish base of the corolla tube and forms a further steep, narrow tubelet around the relatively long stipe of the gynostegium. In *O. longidens* the corolla lobes are ovate to fairly narrowly ovate and their margins are usually ornamented with some cilia. The illustrations of material from Moçambique

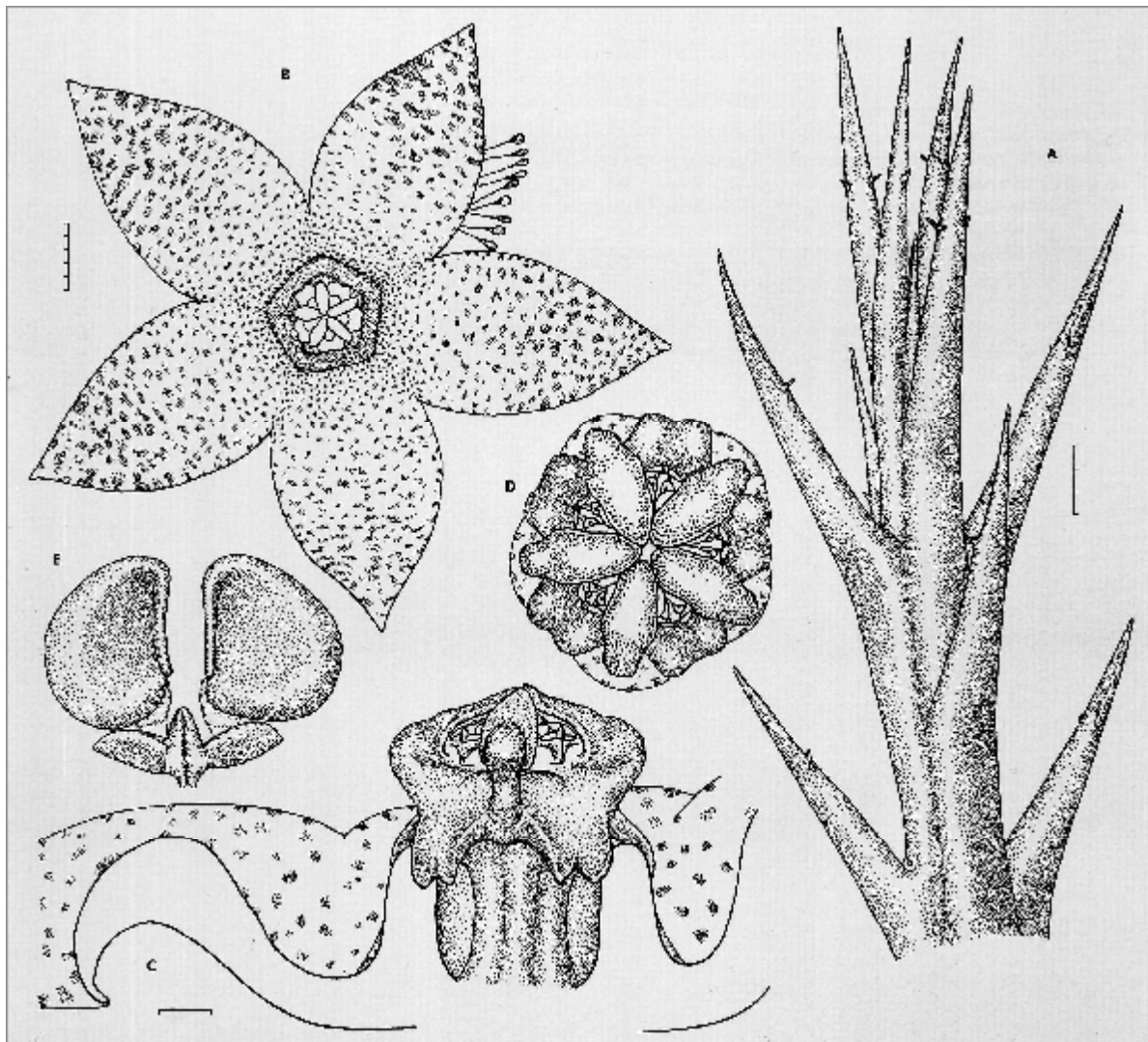


Fig. 10.116. *Orbea longidens*. A, apex of stem. B, face view of flower. C, side view of centre of dissected flower. D, face view of gynostegium on annulus. E, pollinarium. Scale bars: A, 3 mm; B, 5 mm; C, D, 1 mm (at C); E, 0.25 mm (at A). Drawn from: PVB 4449, near Hluhluwe.

ORBEA LONGIDENS



Fig. 10.117. *O. longidens*, PVB 4464, near Mansengwenya.



Fig. 10.118. *O. longidens*, PVB 4449, near Hluhluwe.



Fig. 10.119. *O. longidens*, PVB 4449, near Hluhluwe.

all show no cilia (e.g. Gomes e Sousa 1936) and this is true also of material collected in December 2000, north of Maputo. However, cilia seem mostly to be present in material from northern KwaZulu-Natal, although even there they can be very few and on one freshly opened flower from near Hluhluwe only a single cilium was observed.

The corona consists of relatively short, usually apically notched outer lobes adpressed to the top of the annulus with inner lobes covering the anthers but not rising above them. They are similarly coloured to the corolla.

Orbea longidens differs from *O. macclough-*

linii by the much steeper and more thinly walled annulus surrounding the gynostegium and by the presence of a small corolla tube in the centre of the flower in which this annulus is situated. The stems, with their slender tubercles, are also rather different from those in *O. maccloughlinii*.

History

Orbea longidens was discovered by Mrs. Rose Monteiro in the area around Delagoa Bay (today Baie de Maputo) and sent to Kew in 1883 (Brown 1895). Plants from her collection

were cultivated by Eric D. and W.H. Tillett of Norwich and the figure in the *Gardener's Chronicle* (Anon, 1898) was made from specimens grown by them. The next recorded collection was made by Antonio Gomes e Sousa in November 1934 to the north of Maputo near Mangulane (Gomes e Sousa 1935) and he recorded it several more times around Maputo (Gomes e Sousa & Esteves de Sousa 1947). The species seems to have remained very little known and, as far as one may gather, it was not seen in the living state either by White & Sloane or by Carl Lückhoff.



Fig. 10.120. *O. longidens*, PVB 4464, near Mansengwenya. The stems blend in remarkably well with small tufts of grass (partly removed here), January 1991.

18. *Orbea maculata*

Orbea maculata (N.E. Br.) L.C. Leach, *Excelsa*

Taxon. Ser. 1:49 (1978).

Caralluma maculata N.E. Br., *Fl. Trop. Afr.* 4 (1): 487 (1903).

Type: Botswana, near T'Klakane pits, northern Kalahari, Apr. 1899, Lugard 297 (K).

Dwarf to small succulent, usually consisting of several small clumps (to 100 mm diam.) connected by long rhizomes. Stems 20-100 mm long, 6-15 mm thick (excluding teeth), slender to stout, erect above soil often from horizontal subterranean rhizome up to 500 mm long, grey-green flecked with purple-brown; *tubercles* 4-20 mm long, arranged into 4 obtuse rows along stems with groove between rows, prominent to very prominent, laterally flattened, deltoid, acute to acuminate, usually with pair of deltoid stipular denticles shortly below apex. *Inflorescence* 1 per stem near base, of 1-5 flowers developing in gradual succession from short fleshy peduncle < 5 mm long; *pedicel* 25-50 mm long, $\pm$ 2 mm thick, horizontally spreading then descending with abruptly upturned apex; *sepals* 4-6 mm long, 1.5-2.0 mm broad at base, ovate, acuminate to attenuate. *Corolla* 30-75 mm diam., rotate, very deeply lobed; outside pale

green with purplish spots arranged in longitudinal lines; inside pale greenish yellow to white dotted or irregularly transversely banded with red-purple to maroon (dots often sunken) becoming pinkish to maroon towards centre and sometimes coalescing to solid red-purple towards apices of lobes, smooth to slightly papillate; *tube* 0.5-1.0 mm deep, formed by small thickened annulus around base of gynostegium; *lobes* 12-32 mm long, 6-15 mm broad at base, spreading, slightly recurved towards apices, convex from reflexed margins, oblong, obtuse to subacute, margins in lower two thirds with vibratile flattened clavate white to purple cilia 1.5-3.0 mm long. *Corona* 3.5-1.5 mm tall, 4.5-7.0 mm broad, dome-shaped, pentagonal to circular, raised above annulus on pentagonal stipe 1-2 mm long, sometimes concave beneath and sometimes narrowing into stipe, yellow to orange or pink or maroon; *outer lobes* continuous and disc-like around gynostegium, forming horizontal spreading platform (0.5-2.0 mm wide) below guide-rails (sometimes considerably reduced) with much swollen often somewhat rugulose $\pm$ rectangular ridge 1.5-2.0 mm long (sometimes with crenulate outer margin) behind anthers rising up to meet inner lobes; *inner lobes* < 1.0 mm long, adpressed to and sometimes slightly longer than backs of anthers, deltoid, subacute to obtusely truncate.

Orbea maculata is very widely distributed, occurring intermittently from the western side of the subcontinent near the mouth of the Kunene River to the eastern edge in KwaZulu-Natal. It is also found southwards in Namibia along the edge of the Namib Desert to quite near the border with South Africa, though always remaining outside the region receiving winter-rainfall. From this known distribution, it is reasonable to surmise that it occurs in southern Angola too.

The relatively large flowers which are produced in gradual succession and are usually pressed to the ground, suggest that this species is a typical member of *Orbea*. The remarkable ring-like coronal structure (more developed behind the inner lobes than between them) is unique in the genus and the usually obtuse corolla lobes are also characteristic and unusual in *Orbea*. Molecular data does not place *O. maculata* within *Orbea*, but neither have its relationships with the main 'Orbea-branch' been resolved.

Key to the subspecies of *O. maculata*

1. Corolla somewhat depressed in centre, outer corolla lobes much shorter below guide-rail than part behind inner lobes 18b. subsp. *kakoenensis*
1. Corolla somewhat convex towards centre, outer corolla lobes nearly as long below guide-rail as part behind inner lobes 2.
2. Corona narrowing below into stipe, outer lobes below guide-rail equal in length to part behind inner lobes 18a. subsp. *maculata*
2. Corona not narrowing below but changing abruptly into stipe, outer lobes below guide-rail slightly but noticeably shorter than part behind inner lobes 18c. subsp. *rongeana*

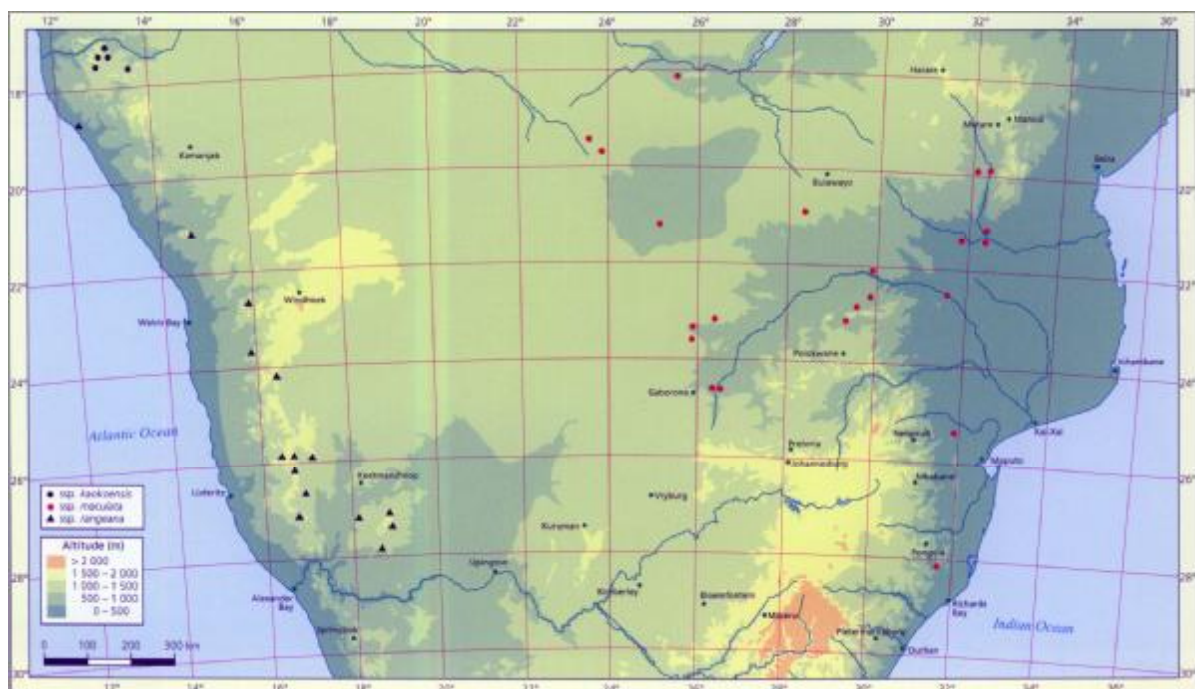


Fig. 10.121. Distribution of *Orbea maculata*.

18a. *Orbea maculata* subsp. *maculata*

Caralluma grandidens L.Verd., Fl. Pl. South Africa 13: t. 518 (1933).

Stapelia grandidens (L.Verd.) P.V.Heath, Calyx 1: 16 (1992).

Lectotype: South Africa, Transvaal, Soutpan, Obermeyer, Schweickerdt & Verdoom 403 (PRE).

Small succulent, usually consisting of several small clumps (to 100 mm diam.) connected by horizontal underground rhizomes up to 500 mm long. Stems 40-100 mm long, 6-15 (-25) mm thick (excluding teeth), slender; tubercles 4-15 mm long, narrowly deltoid, 30-60 mm diam., somewhat convex above towards centre; inside pale greenish yellow dotted (sometimes shortly transversely lined) with red-purple becoming pinkish towards centre and dots usually coalescing to solid red-purple towards apices of lobes, smooth; lobes 14-25 mm long, 6-9 mm broad at base, with white marginal cilia. Corona 4.5-6.5 mm diam., obtusely pentagonal to circular, narrowing into stipe $\pm$ 1 mm long; outer lobes below guide-rail $\pm$ equal in length to part behind inner lobes; inner lobes deltoid and subacute to obtusely truncate sometimes with crenulate margin, rising onto anthers from swollen area where fused to outer lobes.

Distribution and habitat

Subsp. *maculata* is probably the most widely distributed of the three subspecies that are recognised. Leach (1978a) recorded a single collection (other than the type) from Botswana, various gatherings from western, southern and eastern Zimbabwe and several more in South Africa from the northernmost part of the country and along the edge of the Kruger National Park. Subsequently, my own investigations in Botswana proved it to be widely distributed there too, from around Maun to near Gaborone. It is also now known to grow in KwaZulu-Natal near Ulundi. Although it may on occasion be locally quite plentiful, plants are usually rather scattered and the species is somewhat uncommon. Specimens frequently grow in stony ground (often in calcrete) in open and mostly flat bushveld. Over most of its range subsp. *maculata* is associated with the very characteristic, rather open and dry woodland formed by *Colophospermum mopane*. Nevertheless, several collections have been made in other types of bush. For example, around Ulundi in KwaZulu-Natal it occurs on dolerite soils among tufts of grass and scattered *Acacia* bushes and in Botswana it was observed in overgrazed spots with stunted shrubs of *Acacia tortilis*.

Diagnostic features and relationships

Plants of subsp. *maculata* are extremely rhizomatous and a single specimen may often spread for up to 2 sq m. Over this area it will consist of several small clusters of stems (often with only 1-3 stems in a cluster, but occasionally a dense bunch of stems up to 100 mm in diameter may develop) above the ground. These clusters are connected by underground rhizomes which can be anything up to 0.5 m long.

Stems of subsp. *maculata* have long slender teeth which, as in several other similar species, can act as a good camouflage among tufts of grass. The rhizomatous habit of subsp. *maculata*, with laterally flattened tubercles along the stem, readily separate it from other species with slender tubercles such as *O. caudata*, *O. rogersii* or *O. tapscottii*. Only with *O. carnosa* subsp. *keithii* (where they occur together, for example, in South Africa north of the Soutpansberg) and with *O. gerstneri* subsp. *gerstneri* in KwaZulu-Natal could confusion arise. However, in *O. gerstneri* the stems have a different, darker colour and in subsp. *keithii* the tubercles are broader and more strongly laterally flattened.

Florally subsp. *maculata* is immediately recognisable. The flowers are produced in small

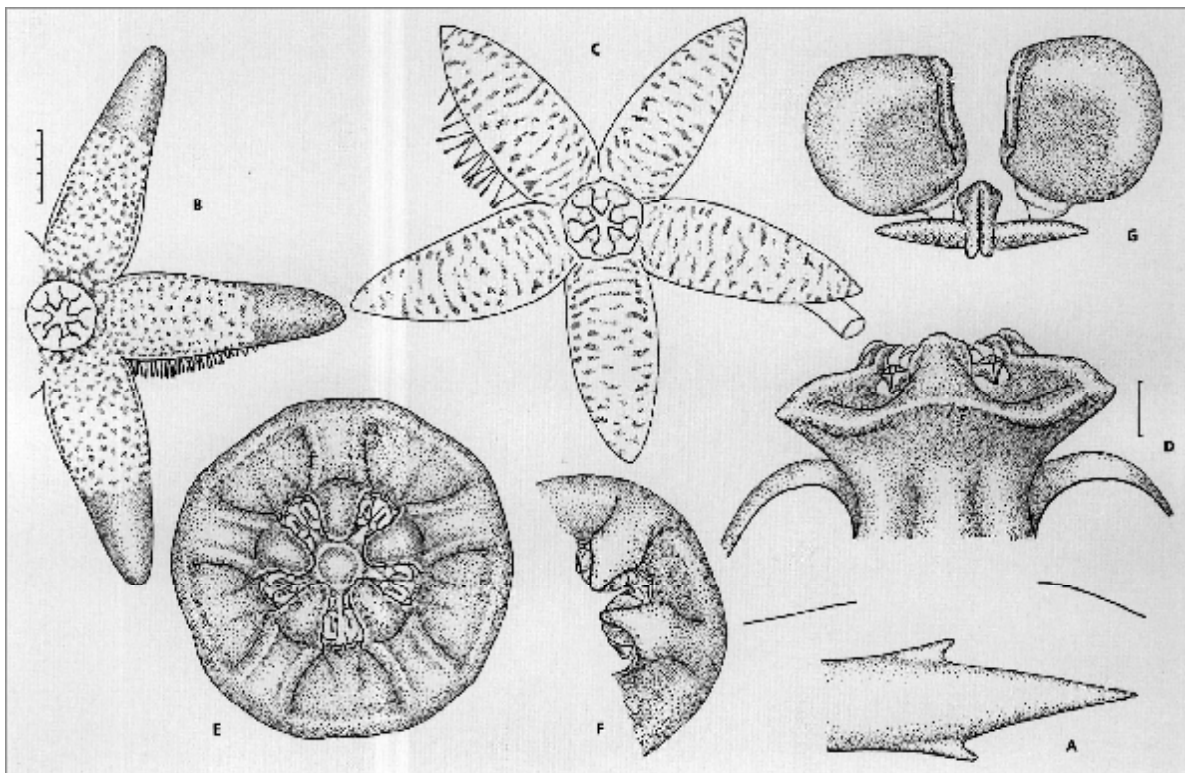


Fig. 10.122. *Orbea maculata* subsp. *maculata*. A, apex of tubercle with stipular ridges. B, C, face view of flower. D, side view of centre of dissected flower. E, F, face view of gynostegium. G, pollinarium. Scale bars: A, 1 mm (at B); B, C, 5 mm (at B); D-F, 1 mm (at D); G, 0.25 mm (at B). Drawn from: A, PVB 7671, near Messina; B, PVB 6986, south of Gweta, Botswana; C-E, G, PVB 4446, Okhukhu, near Ulundi; F, PVB 6435, south of Shoshong, Botswana.

numbers around the base of the stem. The pedicel is relatively long and becomes adpressed to the ground with an abruptly upturned apex so that the flower is also adpressed to the soil and faces upwards. The deeply lobed flowers are very variable in size but are usually finely spotted (and more rarely transversely striped) with red-purple on pale yellow. This spotting covers most of the surface but usually the spots become larger towards the apices of the lobes and coalesce there into a dark red-brown, often somewhat shiny patch. Although a cursory examination of the flower does not show it, the corolla is actually much thickened quite abruptly around the base of the corona into a small annulus.

The corona is peculiar, with the outer lobes forming a ring-like structure which is much more developed behind the anthers than between them. Behind the anthers, this ring is thickened to rise up to the inner lobes and between the inner lobes there is a flat platform beneath the guide-rails. In subsp. *maculata* the thickened parts behind the anthers do not quite reach the level of the anthers and the inner corona lobes rise up from their level onto the anthers. The corona appears to be pressed to the centre of the corolla but actually it is raised slightly above the surface and out of the tube by a thick pedestal beneath it. In subsp. *maculata* the corona gradually narrows into this pedestal.

Leach (1978a) gave various distinctions between *O. maculata* and *O. rangeana*. The most important of these differences are the much thicker stems with shortly deltoid teeth, the broader, more strongly folded corolla lobes and the broader inner corona lobes, all in *O. rangeana*. The position is much confounded by the recently discovered forms in the Kaokoveld. In these the tubercles on the stems are as long as in *O. maculata* or may be even longer but they are also much broader than the tubercles in either *O. maculata* or *O. rangeana*. In plants from the Kaokoveld the stems are fairly thick and the inner corona lobes are intermediate in breadth between the two former species. Consequently they are now treated under one species.

History

Orbea maculata was discovered by Edward J. Lugard in April 1899 at the Bushmen water pits near Lake Ngami during an expedition that he made to the northern Kalahari with his wife, Charlotte Eleanor Lugard. Flowers from this gathering were preserved and taken to Kew and from these the species was described by N.E. Brown in 1903. It was rediscovered in January 1933 just north of the Soutpansberg near Soutpan in Limpopo Province by Obermeyer, Schweickerdt and Verdoorn and this collection was described as *Caralluma grandidens*. Only in 1959 was it first noticed in Zimbabwe and since then records have gradually accumulated over its wide distribution. Material was gathered in KwaZulu-Natal for the first time by Dennis de Kock in 1981.



Fig. 10.123. *O. maculata* subsp. *maculata*, PVB 4446, Okhukhu, near Ulundi.



Fig. 10.124. *O. maculata* subsp. *maculata*, PVB 6435, south of Shoshong, Botswana, an unusually dark-flowered plant.



Fig. 10.125. *O. maculata* subsp. *maculata*, PVB 6986, south of Gweta, Botswana.



Fig. 10.126. *O. maculata* subsp. *maculata*, PVB 6435, south of Shoshong, Botswana. A large specimen which was over 0.3 m in diameter, in habitat, December 1995.

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18b. *Orbea maculata* subsp. *kaokoensis*

Orbea maculata subsp. *kaokoensis* Bruyns, *Aloe* 37:75(2001).

Type: Namibia, Kaokoveld, north-west of Opuwa, Bruyns 4083 (BOL).

Small succulent, usually consisting of several small clumps (to 100 mm diam.) connected by horizontal underground rhizomes up to 0.5 m long. Stems 40-100 mm long, 8-15 mm thick (excluding teeth), often stout; *tubercles* 8-20 mm long, often very broadly deltoid. *Corolla* 50-75 mm diam., usually with centre shallowly depressed; inside pale cream-yellow becoming pale green in upper half of lobes, with sunken maroon spots, spots becoming abruptly larger and coalescing below base of lobes so that centre nearly all dark maroon, smooth; *lobes* 20-32 mm long, 7-15 mm broad at base, with white marginal cilia. *Corona* 6-7 mm diam., pentagonal, raised on pentagonal stipe ± 1.5 -2.0 mm long, convex below but not narrowing into stipe, reddish to yellow; *outer lobes* with part below guide-rail reduced to < 0.5 mm long but $\pm$ as broad as massive entire and roughly square part behind inner lobes; *inner lobes* deltoid and obtuse to oblong and truncate.

Distribution and habitat

This taxon is known only in the higher regions of the Kaokoveld in northern Namibia. It has been found from north-west of Opuwa to

around the Baynes Mountains both on the south-western and north-eastern sides and on the western side of the Otjihipa. It is very likely to occur in the adjacent part of southern Angola.



Fig. 10.127. *O. maculata* subsp. *kaokoensis*, PVB 7996, north-west of Okonguati, Namibia, showing the rhizomatous habit with thin underground stems and the large teeth along the above-ground portions of the stems.

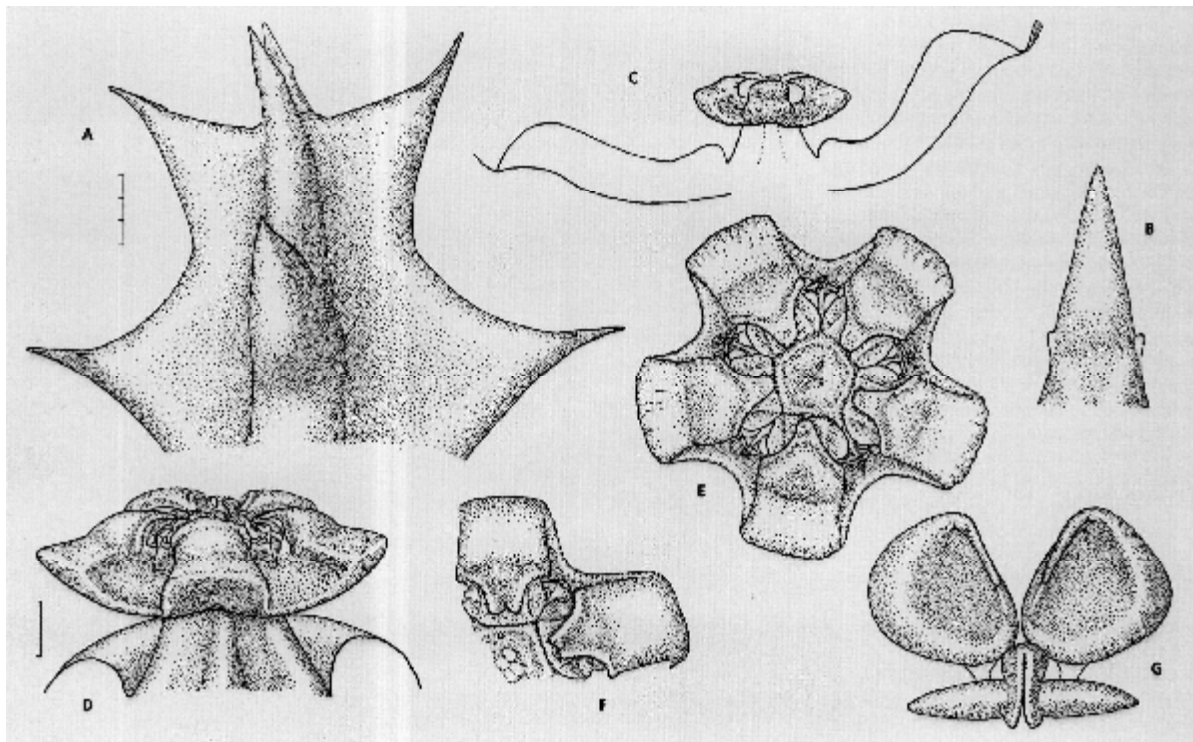


Fig. 10.128. *Orbea maculata* subsp. *kaokoensis*. A, apex of stem. B, apex of tubercle with stipular ridges. C, side view of centre of dissected flower. D, side view of gynostegium. E, F, face view of gynostegium (or part). G, pollinarium. Scale bars: A, C, 3 mm (at A); B, 1 mm (at A); D-F, 1 mm (at D); G, 0.25 mm (at A). Drawn from: F, PVB 5590, north-west of Okonguati, Namibia; rest, PVB 4083, north-west of Opuwa, Namibia.

Plants are of rather scattered occurrence and they generally occur in stony ground among *Colophospermum mopane* and trees of various species of *Acacia*. Specimens have mostly been seen on shale hills (occasionally granite) and were quite often observed in patches of quartz gravel. They have been found from the valleys to some of the higher mountains, at altitudes of between 1 200 and 1 800 m.

Diagnostic features and relationships

In subsp. *kaokoensis* the stems are larger than in either of the other two subspecies. The tubercles may be up to 20 mm long and 15 mm broad at the base so they are much broader than in subsp. *maculata* and longer than in subsp. *rangeana* and they are more like the very robust forms of *O. carnosa* subsp. *keithii* found in the Limpopo Valley north of the Soutpansberg. They have the same rhizomatous habit as the other two subspecies, with small clusters of stems developing at distances of up to 0.5 m from the parent plant and connected to it by slender, horizontal underground runners. Here the underground parts are particularly slender relative to the quite massive above-ground parts.

In all the flowers seen the corolla lobes were spotted and barred with maroon on cream with the spots coalescing to form a dark maroon centre below the bases of the lobes. This dark centre of the flower is somewhat depressed below the level of the lobes so that it is shallowly bowl-shaped. The depressed area is slightly asymmetric, with the deeper side next to the pedicel.

The corona of subsp. *kaokoensis* resembles that of the other two quite closely. The stipe narrows towards the corona as in subsp. *rangeana* and not as in subsp. *maculata*. The parts of the outer corona behind the anthers are broad, almost square and nearly flat on top. They have broad gaps between them (as in subsp. *maculata*) but the part that fills these gaps is greatly reduced and often only slightly visible beneath the guide-rails. As in subsp. *maculata*, the inner corona lobes rise somewhat onto the anthers.

History

Subsp. *kaokoensis* was first observed by a Mr. Venter, the stock inspector for the Kaokoveld until about 1992. He had some plants of it in cultivation in Opuwa and directed me to a locality for it. It has since been located in many other spots around the foot of the Baynes Mountains in the Kaokoveld.



Fig. 10.129. *O. maculata* subsp. *kaokoensis*, PVB 5590, north-west of Okonguati, Namibia.



Fig. 10.130. *O. maculata* subsp. *kaokoensis*, PVB 4083, north-west of Opuwa, Namibia.



Fig. 10.131. *O. maculata* subsp. *kaokoensis*, PVB 8018, near Okombambi, Namibia, in habitat, December 1999.

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18c. *Orbea maculata* subsp. *rangeana*

Orbea maculata subsp. *rangeana* (Dinter & A.Berger) Bruyns, *Aloe* 37: 76 (2001).
Caralluma rangeana Dinter & A.Berger, *Bot. Jahrb. Syst.* 50, Suppl.: 591 (1914), as '*rangei*', *Neue Pflanzen Deutsch-SWAs*: t. 50 (1914).
Orbea rangeana (Dinter & A.Berger) L.C.Leach, *Exeisa Taxon. Ser. 1*: 51 (1978).
Stapelia rangeana (Dinter & A.Berger) P.V.Heath, *Calyx* 1:16 (1992).
Type: Namibia, Kuibis, Dinter 1226 (missing).
Neotype: Namibia, Kanus, April 1913, Dinter 2597a (SAM).
Piarranthus strejyanus Nel, *Desert PL Life* 21: 99 (1949).
Type: Namibia, Bullsport, Strey (missing).
Lectotype: *Desert PL Life* 21: upper fig. on page 100.
Caralluma maculata var. *brevidens* H. Huber, *Mitteil. Bot. Staatssamml. München* 4: 33 (1961).
Type: as for *O. maculata* subsp. *rangeana*.

Dwarf succulent usually consisting of several small clumps mostly not exceeding 60 mm diam. connected by horizontal underground rhizomes up to 300 mm long. Stems 20-80 mm long, 6-15 mm thick (excluding teeth), often stout, *tubercles* 4-7 mm long, often shortly and broadly deltoid. *Corolla* 32-70 mm diam., somewhat convex above towards centre; inside greenish yellow to white transversely marked and spotted with broken irregular bands of red-purple to maroon, smooth or with few short stiff clavate papillae on disc and towards sinuses of lobes; *lobes* 12-26 mm long, 4-10 mm broad at base, with purple marginal cilia. *Corona* 5-7 mm diam., obtusely pentagonal, raised on stipe 1.5-2.0 mm tall, slightly concave below and not narrowing into stipe, yellow, orange-red or maroon; *outer lobes* with part below guide-rail considerably narrower than massive part behind inner lobes; *inner lobes* ± deltoid with apex obtuse to irregularly shallowly bilobed.

Distribution and habitat

Only found in Namibia, *O. maculata* subsp. *rangeana* is known now from almost the entire length of the territory. In the south it occurs from around the base of the Great Karas Mountains westwards to the Huib Plateau (north-east of Witpütz). Collections have also been made along the northern aspect of the Tiras Mountains and in the Schwarzrand. North of this there are scattered records along the eastern edge of the Namib Desert from around the Naukluft, from a single collection near Usakos and several collections that have been made on the upper parts of the Brandberg slightly further north (Bruyns 1990b; Craven & Craven 2000). Very recently it was also recorded south-west of Orupembe on the edge of the Skeleton Coast Park, some 150 km south of the Kunene River.

Subsp. *rangeana* grows on stony ground, sheltering under small bushes or between rocks. It has been found at altitudes of about 350 m on the Skeleton Coast to over 2 400 m in the upper reaches of the Brandberg. Plants are almost always found in granitic areas but have also been collected on shales and on dolomite.

Diagnostic features and relationships

In subsp. *rangeana* the stems form clumps up to 60 mm diameter with some of them spreading underground for up to 300 mm to form new clusters. They are green to grey-green, depending on the extent to which they are exposed, faintly mottled with dark green to purple and have prominent broadly deltoid tubercles each



Fig. 10.132. *O. maculata* subsp. *rangeana*, PVB 4181, Schwarzrand near Bethanie, Namibia.



Fig. 10.133. *O. maculata* subsp. *rangeana*, PVB 3532, eastern flank of the Great Karas Mountains, Namibia, in habitat, January 1989, after good rain.

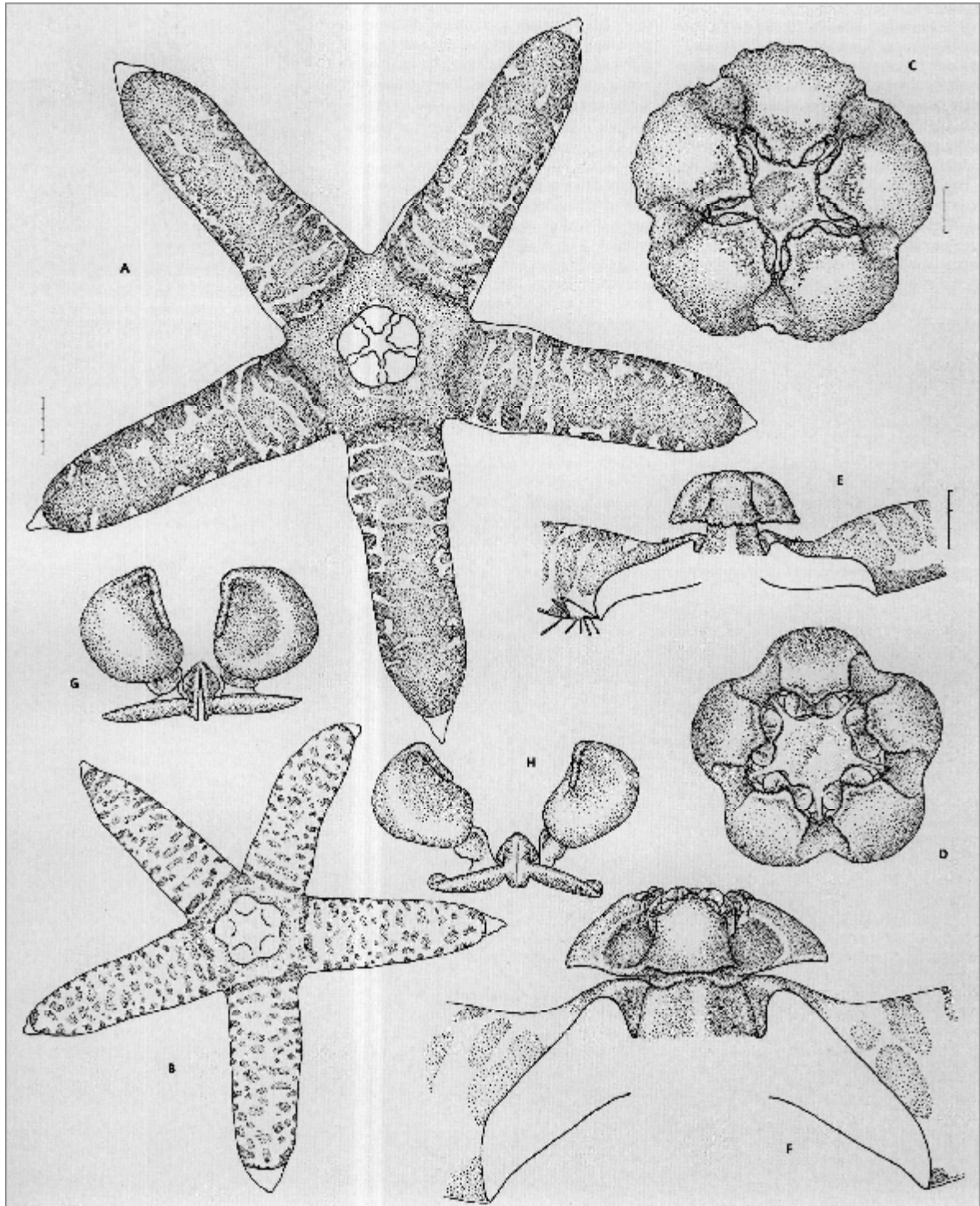


Fig. 10.134. *Orbea maculata* subsp. *rangeana*. **A, B**, face view of flower. **C, D**, face view of gynostegium. **E, F**, side view of centre of dissected flower. **G, H**, pollinarium. Scale bars: A, B, 5 mm (at A); C, D, F, 1 mm (at C); E, 3 mm; G, H, 0.25 mm (at E). Drawn from: A, C, E, G, *PVB 3063*, upper slopes of the Brandberg, Namibia; B, D, F, H, *PVB 3547*, Pieterskloof, Great Karas Mountains, Namibia.

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tapering to a small tooth.

Florally subsp. *rangeana* is more similar to subsp. *maculata* than the rather different looking stems would suggest. The flowers are a little larger but are similarly spotted with maroon on pale yellow. Although some of them are indistinguishable in their colouring from flowers in subsp. *maculata*, many are far more densely spotted and some very large and dramatically mottled ones, where the colours were deep maroon on white, have been collected on the Brandberg. In these the centre of the flower was also maroon but usually it is the same as the rest. The lobes are often somewhat reflexed, pushing the centre of the flower forwards, and their margins are usually ornamented with purple cilia.

As in subsp. *maculata*, the corona of subsp. *rangeana* is raised out of the small corolla tube (formed by the annulus) on a trunk-like pedestal. However, whereas in subsp. *maculata* the stipe widens into the base of the gynostegium, here the base of the corona is somewhat concave and has small flaps of tissue surrounding the top of the stipe. Once again, the outer corona is ring-like with large, thickened portions behind the inner lobes. In subsp. *rangeana* these thickened

areas are much broader than the parts between them, which are very small indeed. They rise up from the edge of the corona and reach the level of the anthers so that the inner corona lobes are not clearly distinguishable from them, as they are in subsp. *maculata*.

History

Subsp. *rangeana* was discovered by M. Kurt Dinter in January 1910 at Kuibis, about 30 km east of Aus, in southern Namibia. Soon afterwards (in April 1913) he collected it again at Kanus between Grünau and Karasburg. He and Alwyn Berger described it jointly in 1914, among the small selection of 'new' succulents that they contributed to the celebratory supplement of the *Botanische Jahrbücher* which was published for the 70th birthday of Adolf Engler. They named it in honour of Paul Range, a geologist who contributed considerably to the knowledge of the botany of southern Namibia. Dinter and Berger also mentioned on this occasion that its corona was so unusual that this was nearly enough to justify placing it in a separate genus. G.C. Nel redescribed it in 1949 from material collected by R.G. Strey on



Fig. 10.135. *O. maculata* subsp. *rangeana*, PVB 3063, upper slopes of the Brandberg, Namibia. This plant has unusually large and deeply coloured flowers.

his farm Bullsport, at the south-eastern corner of the Naukluft. Nel placed his 'new' species in *Piранthus* on account of the unusual corona. Leach (1978a) was the first to consider that this taxon and *O. maculata* might be related to species such as *O. variegata*, though it was not included among the first group of species that he moved to *Orbea* (Leach 1975).



Fig. 10.136. *O. maculata* subsp. *rangeana*, PVB 5699, west of Helmeringhausen, Namibia, flowering in habitat, March 1993.

19. *Orbea paradoxa**Orbea paradoxa* (L.Verd.) L.C.Leach, *Excelsa Taxon.*

Ser. 1: 55 (1978).

Stultitia paradoxa L.Verd., *Fl. Pl. South Africa* 17: t. 677 (1937).*Stapelia paradoxa* (L.Verd.) P.V.Heath, *Calyx* 1:16 (1992).Lectotype: Moçambique, Ressano Garcia, *Blignaut & Van der Merwe* 403 (PRE).

Dwarf succulent forming small clumps (up to 150 mm diam.) connected underground by rhizomes up to 100 mm long. *Stems* 30-60 mm long, 4-8 mm thick (excluding teeth), slender, above-ground parts erect, grey-green

mottled with purple-brown; *tubercles* 5-15 mm long, arranged into 4 obtuse rows along stems with groove between rows, tapering into prominent conical acute tooth often somewhat flattened above towards apex, with 1-3 pairs of ascending also sometimes somewhat flattened denticles shortly below apex. *Inflorescence* 1 per stem near base, of 1-3 extremely foul-smelling flowers developing successively on peduncle < 5 mm long; *pedicel* 8-10 mm long, spreading with ascending apex, holding flower facing upwards; *sepals* 4-6 mm long, 1.5 mm broad at base, ovate-acuminate. *Corolla* 18-32 mm diam., campanulate, rigidly fleshy, outside smooth, pale green with longitudinal purplish lines; inside smooth and somewhat shiny, with irregular transverse pink to dark red or purple markings on white or cream around and below

bases of lobes with markings fading and becoming finer towards tips where background colour faintly greenish, dark to pale maroon on annulus and inside tube, sometimes with white ring just outside mouth of tube; tube 6-8 mm long, 7 mm broad, cupular, slightly constricted at mouth by prominent inward-pointing fleshy pentagonal to circular annulus 2-3 mm tall, with stiff erect acute bristles up to 0.75 mm long towards base around gynostegium; *lobes* 6-10 mm long, 6-10 mm broad at base, ovate-deltate, slightly convex above, with clavate vibratile cilia < 1.5 mm long along margin of lower half. *Corona* 2.5-3.0 mm tall, 5-6 mm broad, raised slightly above base of tube on very short (0.5 mm) pentagonal stipe; *outer lobes* 1.5-2.0 mm long, 1.8-2.0 mm broad, ± rectangular or ovate with deltoid upturned apex, deeply concave on upper surface

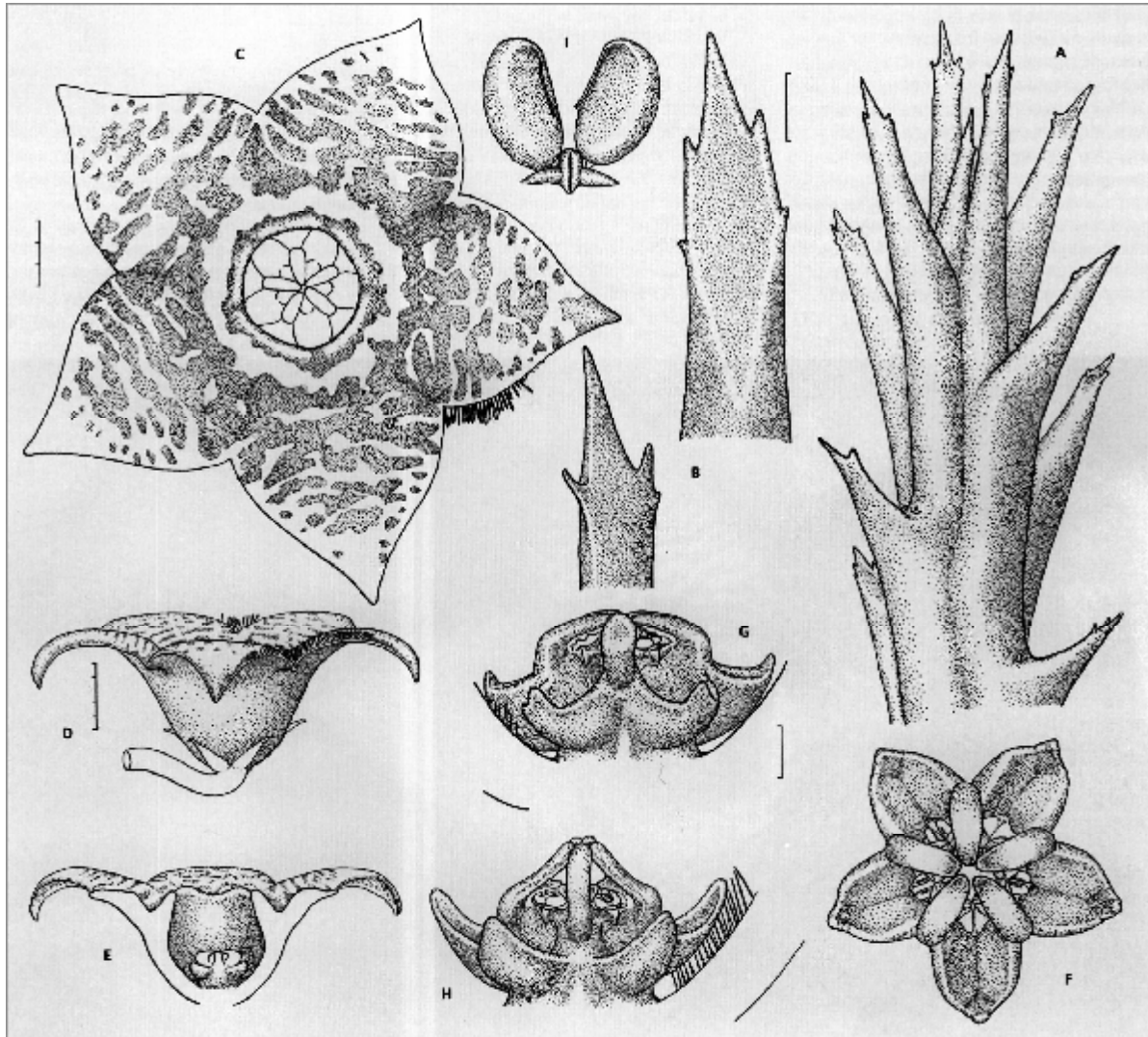


Fig. 10.137. *Orbea paradoxa*. A, apex of stem. B, apex of tubercle with stipular ridges. C, face view of flower. D, side view of flower. E, side view of dissected flower. F, face view of gynostegium. G, H, side view of gynostegium. I, pollinarium. Scale bars: A, C, 3 mm (at C); B, 1 mm; D, E, 5 mm (at D); F-H, 1 mm (at G); I, 0.25 mm (at B). Drawn from: H, Peckover, Makhatini Flats (no specimen); rest, PVB 4465, south of Ndumu.

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especially towards base, yellow suffused with brown to dark red towards base and along margins to wholly maroon above; *inner lobes* ± 1 mm long, adpressed to backs of anthers, exceeding them and meeting in centre sometimes rising in small column there, linear, obtuse, with slight dorsal swelling towards base.

Distribution and habitat

Orbea paradoxa is found for a distance of a little over 200 km in a relatively narrow band along the foot of the Lebombo Mountains in the adjoining parts of Moçambique, Swaziland and South Africa. Records have been made from around Komatipoort in South Africa and Ressano Garcia in Moçambique southwards to Makhatini and Mkuzi in KwaZulu-Natal.

Plants grow mainly in flat areas below 300 m above sea level and frequently occur in black turf soils or dark brown loam in places which become seasonally waterlogged. As Leach (1978a) mentioned, he encountered them in large numbers around the edges of seasonal pans near Catuane in southern Moçambique in association with *Euphorbia knuthii* and *Acacia xanthophloea*. South of Ndumu in KwaZulu-Natal they grow under similar circumstances with *E. knuthii* and *E. grandicornis*, the plants mingling with small grasses and the stems of *E. knuthii*, which also has a rhizomatous habit.

Diagnostic features and relationships

Plants of *O. paradoxa* are extremely rhizomatous, forming small clumps of erect stems above the ground and spreading by means of horizontal underground runners. Here the stems are fairly slender but have relatively short tubercles, which are mostly not more than 6-8 mm long. These tubercles are distinctly flattened above towards the apex and this flattened part constitutes the rudimentary leaf. Towards the base of this flattened area the margins are extended into one to three spreading toothlets on each side (i.e. up to six toothlets per tubercle). This multitude of small denticles around the apex of the tubercle immediately distinguishes this species from any other in the area.

The flowers of *O. paradoxa* are fairly small but make up for this by having an unusual colouring and emitting a very foul smell of rotten meat. Around the bases of the lobes and on the short united part they are transversely and boldly mottled with reddish on a cream background, with the markings becoming smaller and the darker colour fading beyond the middle of the lobes to become eventually a uniform insipid greenish. Around the mouth of the tube there may be a striking white ring and the inside of the tube is a deep to pale maroon. The interior is smooth and quite shiny except

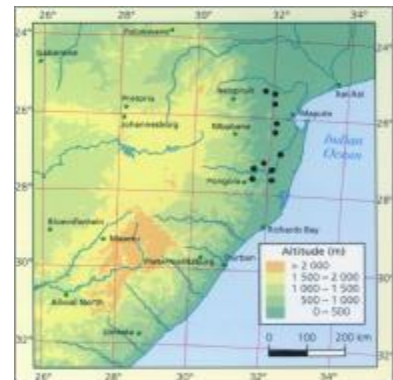


Fig. 10.138. Distribution of *Orbea paradoxa*.

for fine papillae near the tips of the lobes and short hairs in the base of the tube. This whole arrangement, with its colouring and evil smell, somewhat resembles a festering wound on the skin of an animal.

In *O. paradoxa*, below the bases of the lobes, the corolla descends into the tube which, from the outside of the flower, has a more or less funnel-like shape. On the inside, the tissue is much thickened and there is an annulus



Fig. 10.139. *O. paradoxa*, Peckover, Makhatini Flats.



Fig. 10.140. *O. paradoxa*, PVB 4465, south of Ndumu.



Fig. 10.141. *O. paradoxa*, PVB 4465, south of Ndumu.

which rises out of the tube and projects inwards as a thin wall, thereby considerably constricting the mouth of the tube. The shape of this annulus is such that, on the inside, the tube is more or less urceolate. The annulus has an undulating margin which may be very strongly pentagonal but also can be nearly circular.

The corona is seated on a very short stipe in the base of the corolla tube. It consists of short, yellowish to maroon outer lobes which are channelled above and spread out parallel to the base of the tube. The relatively narrow, yellow inner lobes are fairly short and always seem to have obtuse, rounded apices which just meet in the centre or rise in a small column. The inside and the rims of the outer lobes are shiny with a covering of thick, viscous nectar.

This species is somewhat anomalous and Leach (1978a) considered it to be related to *O. longidens* and also to *Pachycymbium keithii*, so that it did not fit very well into his generic arrangement, where he placed these two species in separate genera. The flowers are rather on the small side for *Orbea* but he argued that *O. paradoxa* shared many characteristics in the stems, the corolla and the corona with other species that he placed in *Orbea*. Recent studies also place *O. paradoxa* clearly in *Orbea* and the molecular data suggest that it may be related to *O. rogersii*.

History

The first record of *O. paradoxa* was made by F. Jacob Gerstner near Magut in KwaZulu-Natal in 1928. Plants were collected again in March 1936 near Ressano Garcia in Moçambique by H. Blignaut & F.Z. van der Merwe and it was from this material that it was described as *Stultitia paradoxa* in 1937 by Verdoorn.

20. *Orbea cooperi*

Orbea cooperi (N.E. Br.) L.C. Leach, *Kirkia* 10: 291 (1975).

Stapelia cooperi N.E. Br., *Fl. Cap.* 4 (1): 974 (1909).

Stapeliopsis cooperi (N.E. Br.) E. Phillips, *Fl. Pl. South Africa* 12: t. 445 (1932).

Stultitia cooperi (N.E. Br.) E. Phillips, *Fl. Pl. South Africa* 13: sub t. 520 (1933).

Lectotype: South Africa, Cape, 2 miles east of Conway Station, *N.S. Pillans* 181 (BOL, holo.; K, iso.).

Dwarf succulent forming dense clump 60-120 mm tall and 20-60 mm broad, not rhizomatous. Stems 20-60 mm long, 5-10 mm thick (excluding teeth), ascending to erect, green marked with brown to purple patches and lines; *tubercles* 4-7 mm long, arranged into 4 obtuse rows along stem with groove between rows, tapering into ascending to spreading conical and laterally slightly flattened acute tooth, with minute denticle on each side towards apex. *Inflorescence* 1 per stem near base, of 1-3 (-10) flowers developing in gradual succession, sessile or with peduncle up to 15 mm long, with several short deltoid often laterally toothed bracts 1-2 mm long; *pedicel* 6-12 mm long, 2.0-2.5 mm thick, ascending and holding flower facing partly upwards or horizontally; *sepals* 3-5 mm long, 1.5 mm broad at base, ovate or ovate-lanceolate, acuminate. *Corolla* 22-33 mm diam., rotate; outside smooth, pale green, with 3-5 purplish veins on lobes; inside irregularly ± transversely rugulose with short ridges and tubercles, rugosities becoming denser towards and on annulus but vanishing inside tube, rugosities pale yellow and areas between them pale purple brown; *tube* 1.0-1.5 mm long, 4-5 mm broad, cupular, formed by raised cushion-like convex annulus, containing base of gynostegium only, with dark purple-brown patch in base but no bristles; *lobes* 10-14 mm long, 8-10 mm broad at base, spreading to recurved, ovate, acute, somewhat convex towards apex from slightly recurving margins, with vibratile clavate purple marginal cilia up to 2 mm long on

basal half of lobes. *Corona* 4 mm tall, 5 mm broad, ± without basal stipe, red to deep maroon (darker on outer lobes) to pale yellow flecked with maroon; *outer lobes* < 1 mm long, spreading and resting upon side of tube near mouth, broadly rectangular to deltoid, usually emarginate and with triangular medial notch dividing it into short obtuse lobules, edges raised up towards base and fused to lower backs of inner lobes; *inner lobes* 2.0-3.5 mm long, adpressed to backs of anthers then connivent-erect and sometimes recurved, with apical part terete to slightly clavate, broadly ovate, oblong or ovate-oblong, entire or with 1-2 teeth on each side, sometimes with small irregular obtuse dorsal projection near base.

Distribution and habitat

Orbea cooperi is widely distributed in South Africa from the arid parts of the Northern Cape south-west of Kakamas (on the eastern flank of 'Bushmanland') via Prieska eastwards to Kimberley and southwards to around Cradock in the Eastern Cape. It also occurs in the Free State from east of Kimberley to near Winburg and southwards to Fauresmith.

Specimens of *O. cooperi* are almost always found on stony ground among rocks or under small karroid bushes and, towards the western edge of the distribution, often under shrubs of *Rhigozum trichotomum* (driedoring).

Diagnostic features and relationships

The stems of *O. cooperi* are mostly no more than 50 mm tall and are grouped into dense clumps which are usually fairly small (up to 100 mm across), though these clumps can, on occasion, reach 0.5 m in diameter. The stems are green, marked, often strongly, with purple so that they can appear quite dark. Their relatively short tubercles are arranged into four obtuse

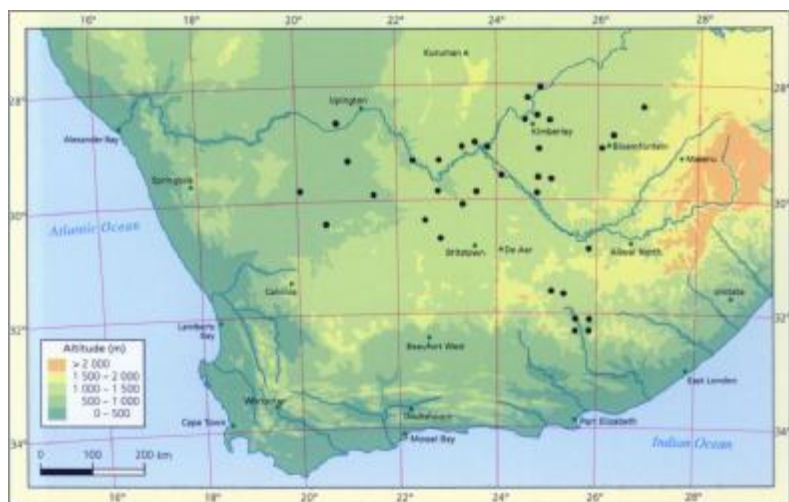


Fig. 10.142. Distribution of *Orbea cooperi*.

ORBEA COOPERI

rows and each is tipped by a tooth which is slightly flattened above and subtended by two small denticles. In most respects plants of *O. cooperi* are therefore very similar to those of *O. variegata* or *O. verrucosa*, except for their darker colour.

However, the flowers are considerably different from those of either *O. variegata* or *O. verrucosa*. In *O. cooperi* the whole of the inside of the flower is covered with fine, broken, transverse ridges. The tops of these ridges are pale yellow and the areas between them purple-brown. This darker colour is fairly obvious on the lobes where the ridges are quite widely spaced. However, towards the centre (and particularly on the annulus), they become much finer and extremely close together and this area has a generally paler colour as a consequence. The flower is usually not more than 30 mm across and is flat to somewhat reflexed, with a (sometimes only slightly) raised, thickened, cushion-like annulus in the centre which forms the sides of a small corolla tube. This tube is short and only contains the base of the

gynostegium, with the outer corona lobes rising and spreading to rest on its mouth. The dense cluster of hairs found in the base of the tube in some species (such as *O. variegata*) is missing here entirely, though traces of it remain around the base of the tube in the form of a dark patch with somewhat raised cells.

In some cases the entire corona is maroon and then it contrasts strongly with the pale annulus. It may also be pale yellow speckled with maroon and then it closely matches the colour of the flower. The outer lobes are usually broad and short, with an apical notch in the middle. The inner lobes are broad in the lower half, often so as to cover the anthers and hide the pollinia. Above this they narrow abruptly into an ascending and slender tip. The whole lobe is mostly less than 3.5 mm long, with the upper slender part at most equalling the lower broader part.

Orbea cooperi shares many features with *O. tapscottii* and the differences between them are discussed under the latter.

History

Orbea cooperi was discovered by Thomas Cooper, who was sent from England to the then Cape Colony by W. Wilson Saunders to collect plants for his garden in Reigate, south London. Cooper collected the species somewhere near Cradock, apparently between Christmas 1860 and late January 1861.

N.E. Brown (1907-09) mentioned, after describing it as *Stapelia cooperi*, that it 'does not quite agree with *Stapelia* or any other genus in structure, but I do not know where else to place it'. In 1932 it was moved to a new genus *Stapeliopsis* E. Phillips but, since this was illegitimate, Phillips then described another new genus *Stultitia* E. Phillips for it, alluding in this name to the mistake he made by describing the genus *Stapeliopsis* E. Phillips. Along with various other species, it was moved to *Orbea* by Leach in 1975.

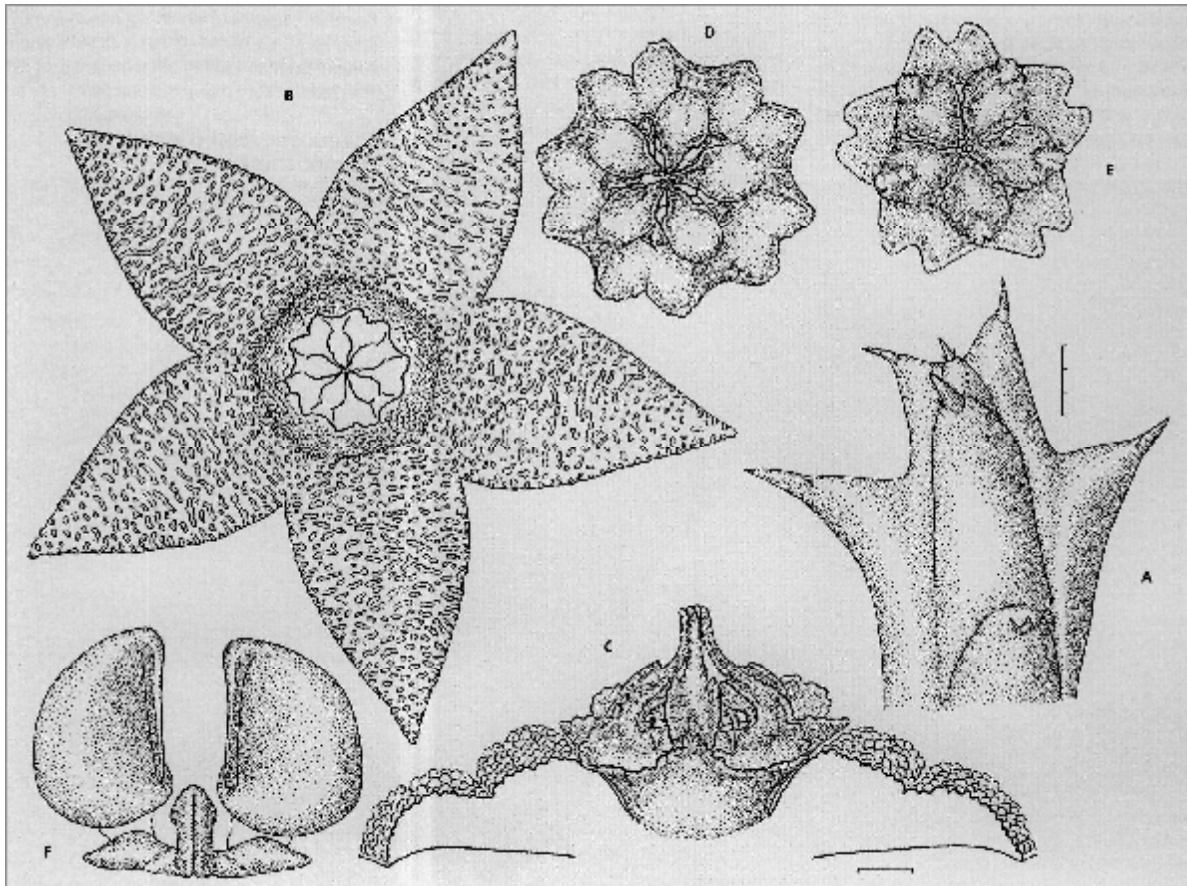


Fig. 10.143. *Orbea cooperi*. A, apex of stem. B, face view of flower. C, side view of centre of dissected flower. D, E, face view of gynostegium. F, pollinarium. Scale bars: A, B, 3 mm (at A); C-E, 1 mm (at C); F, 0.25 mm (at A). Drawn from: A-D, F, PVB 3043, south of Prieska; E, PVB 7476, Winburg.



Fig. 10.144. *O. cooperi*, PVB 7476, Winburg.



Fig. 10.145. *O. cooperi*, PVB 7476, Winburg, with much darker-coloured corona than the previous.



Fig. 10.146. *O. cooperi*, PVB 3043, south of Prieska.

21. *Orbea tapscottii*

Orbea tapscottii (L.Verd.) L.C.Leach, *Kirkia* 10: 291 (1975).

Stapelia tapscottii L.Verd., *Bull. Misc. Inform.* 1927: 357 (1927).

Stultitia tapscottii (L.Verd.) E.Phillips, *Fl. Pl. South Africa* 13: t. 520 (1933).

Type: Botswana, Lobatsi, Tapscott (K, holo.; KMG, iso.).

Succulent forming dense clump 60-120 mm tall and 20-500 mm broad, not rhizomatous. Stems 50-120 mm long, 5-10 mm thick (excluding teeth), erect, green marked with brown to purple patches and lines; *tubercles* 10-25 mm long, arranged into 4 obtuse rows along stem with groove between rows, tapering into ascending to spreading conical and laterally slightly flattened slender tooth, with minute denticle on each side towards apex. *Inflorescence* 1 per stem near base, of 1-3 (-10) flowers developing in gradual succession, sessile or with peduncle up to 15 mm long, with several short deltoid often laterally toothed bracts 1-2 mm long; *pedicel* 6-12 mm long, 2.0-2.5 mm thick, ascending and holding flower facing partly upwards or horizontally; *sepals* 3-5 mm long, 1.5 mm broad at base, ovate or ovate-lanceolate, acuminate. *Corolla* 22-60 mm diam., rotate, outside smooth, pale green, with 3-5 purplish veins on lobes; inside pale brown or purple-brown to red between cream ridges; tube 1.0-1.5 mm long, 4-5 mm broad, cupular, formed by raised cushion-like convex annulus, containing base of gynostegium only, with dark purple-brown patch in base but no bristles; *lobes* 10-20 mm long, 8-13 mm broad at base, spreading to recurved, with vibratile marginal cilia up to 3 mm long on basal half of lobes. *Corona* 4 mm tall, 5 mm broad, ± without basal stipe, red to deep maroon (darker on outer lobes) to pale yellow flecked with maroon; outer lobes < 1 mm long, spreading and resting upon side of tube near mouth, deltoid with small apical notch, maroon with pale yellow margins, edges raised towards base and fused to lower backs of inner lobes; *inner lobes*



Fig. 10.147. Sydney Tapscott, after whom this species was named, c. 1940 (courtesy Christopher Tapscott).

4-5 mm long, adpressed to backs of anthers then connivent-erect and diverging towards clavate-tuberculate tips, entire or with 1-2 lateral teeth and often with erect and somewhat laterally flattened dorsal horn (< 1 mm long) below middle, pale yellow with maroon margins and maroon apices, sometimes with small irregular obtuse dorsal projection near base.

Distribution and habitat

Orbea tapscottii is fairly common in south-eastern Botswana from Lephephe to Lobatse. In South Africa it is more widely distributed from Rustenburg to the area south of the Soutpansberg. A few records exist from further east, namely near Pretoria and near Groblersdal.

Orbea tapscottii will sometimes be found among short grasses under an open canopy of trees but it usually seems to prefer growing under short bushes (often shrubs of *Acacia tortilis*) in overgrazed, more exposed patches, where it can become quite common. Plants grow in flat areas in sandy to gravelly ground and sometimes occur on patches of shallow sand overlaying calcrete.

Diagnostic features and relationships

In specimens of *O. tapscottii* the stems are generally densely packed together and may form clumps up to 0.5 m in diameter. The stems have long, slender, ascending, sharp-looking (but actually soft) tubercles up to 25 mm long, which are usually streaked with purple along their sides and into the grooves between the angles. The length of these tubercles and the consequently grass-like appearance of the stems creates a very different impression from *O. cooperi* (and is very similar to *O. rogersii*, with which it may occur socially).

In their flowers *O. tapscottii* and *O. cooperi* differ only slightly. The flowers of *O. tapscottii* are a little larger and are generally paler, with the ridges more spaced and the colour between them a paler brown to red. *Orbea tapscottii* has a generally larger and more clearly defined annulus which forms a raised, pentagonal cushion with well-defined edges, while in *O.*

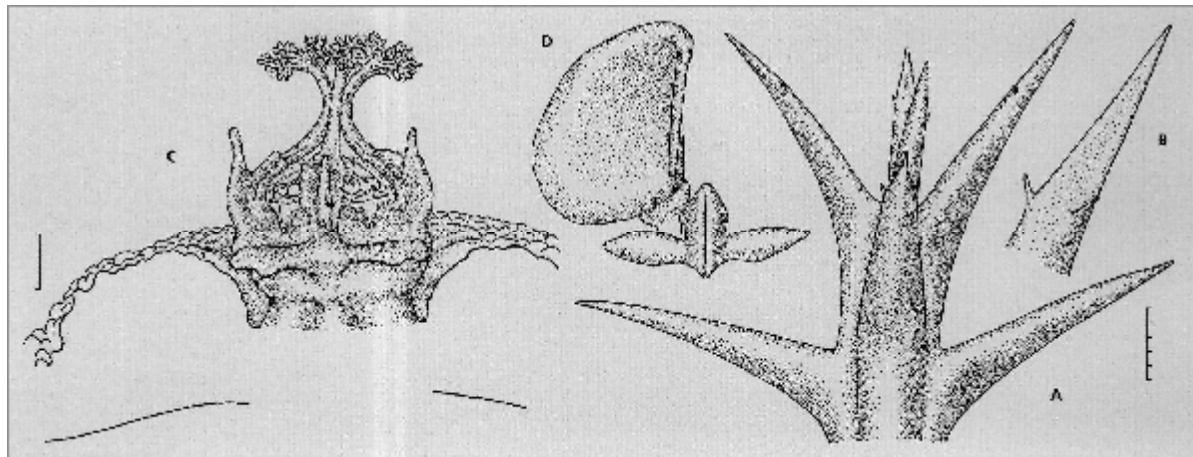


Fig. 10.148. *Orbea tapscottii*. A, apex of stem. B, apex of tubercle with stipular denticles. C, side view of centre of dissected flower. D, part of pollinarium. Scale bars: A, 5 mm; B, 1 mm (at A); C, 1 mm; D, 0.25 mm (at A). Drawn from: A-C, PVB 6557, Ga-Mankodi, south of Blouberg; D, PVB 6412, Boatlaname, Botswana.

cooperi it tends to merge into the surface of the corolla.

As in *O. cooperi*, the outer corona is mostly-maroon but the inner is yellow with maroon edges. Each inner lobe has the same broad base as in *O. cooperi* that sometimes covers the anthers completely, but in *O. tapscottii* it is up to 5 mm long. Here the extra length goes into the much longer, slender upper part, which considerably exceeds the broader, lower part. The five inner lobes rise together in a column above the centre of the flower and sometimes diverge above. Each of them terminates in a thickened, distinctly papillate knob.

History

Orbea tapscottii was first collected by Sidney Tapscott (born Barkly West 25 Nov. 1886, died Simonstown 28 Aug. 1943). Tapscott went to school at Christian Brothers' College in Kimberley and graduated from the University of Cape Town in surveying, after which he studied mining geology at the University of the Witwatersrand. After farming for a time near Riverton Station (near Kimberley), he worked from 1930 as a surveyor on N'Kana mine at Kitwe in Zambia. He found *O. tapscottii* near Lobatse in Botswana in December 1924. These plants were initially thought, by the authorities at Kew, to belong to *Orbea cooperi*, but were later described as a distinct species. Tapscott was a keen natural historian, who collected succulents extensively (his collection was later housed at the Karoo Garden at Whitehill). He also had a marine fossil *Notocaris tapscottii* named for him (Mary Moore, Christopher Tapscott, pers. comm. Nov. 2003).

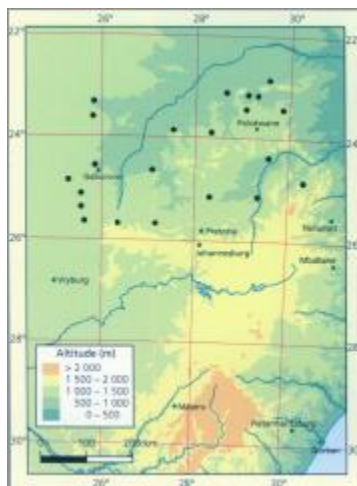


Fig. 10.151. Distribution of *Orbea tapscottii*.



Fig. 10.149. *O. tapscottii*, PVB 6565, west of Vivo, in habitat, January 1996.



Fig. 10.150. *O. tapscottii*, PVB 6412, Boatlaname, Botswana.



Fig. 10.152. *O. tapscottii*, PVB 6565, west of Vivo, cuttings showing the comparatively long teeth along the stems, in habitat, January 1996.

ORBEA UMBRACULA

22. *Orbea umbracula*

Orbea umbracula (M.D.Henderson) L.C.Leach,
Kirkia 10: 291 (1975).

Stultitia umbracula M.D.Henderson, *Fl. Pl. Africa* 35:
t.1374 (1962).

Stapelia umbracula (M.D.Henderson) P.V.Heath,
Calyx 1:16(1992).

Type: Zimbabwe, Bikita distr., Moodies Pass, Leach
& Pienaar 5584 (PRE).

Dwarf succulent forming small clump to 150 mm diam., rarely rhizomatous. Stems 40-100 mm long, 6-10 mm thick (excluding teeth), slender, erect to shortly decumbent, grey-green flecked with purple; tubercles (6-) 10-20 mm long, arranged loosely into 4 obtuse rows along stem $\pm$ without groove between rows, tapering into long slender conical and attenuate ascending-spreading tooth usually with pair of $\pm$ erect slender denticles (up to 1 mm long) 5-8 mm below apex. Inflorescence 1 per stem below middle, of 1-8 flowers developing successively from erect peduncle up to 10 mm long and 5 mm thick, flowers often opening at or shortly above level of stem-apices; pedicel 15-40 mm long, 1.5-2.0 mm broad at base, erect to spreading,

holding flower facing upward or outwards; sepals $\pm$ 6 mm long, 2 mm broad at base, ovate, acuminate. Corolla 30-45 mm diam. when fully spread out, with lobes very strongly reflexed so that tips sometimes nearly clasping pedicel; outside glabrous, grey- to yellow-green; inside minutely papillate, dull maroon to brown becoming shiny with yellowish markings on lobes; tube $\pm$ 2 mm long, 3 mm broad, formed by smooth and very abruptly raised fleshy convex annulus in centre (sides $\pm$ 2 mm thick); lobes $\pm$ 16-20 mm long, 7-9 mm broad at base, ovate, acute, transversely lightly rugulose especially towards apices, margins folded back so that convex above, with fine rigidly fixed usually whitish marginal cilia < 1 mm long (except towards apices). Corona 7 mm tall, 4.5-7.5 mm broad, raised slightly above annulus by stout stipe 2-3 mm long; outer lobes $\pm$ 1.5-2.0 mm, spreading to slightly recurved over rim of annulus, $\pm$ subquadrate, with 2 raised radial ridges bounding lower central area which is produced into acute to rectangular tooth slightly exceeding rest of truncate apex, dull maroon to brown and darker on raised ridges; inner lobes 4-5 mm long, adpressed to backs of anthers and there dorsiventrally flattened ± 1 mm broad and oblong-ovate, above this nearly terete and connivent then recurved with clavate-tuberculate apex, dorsally near

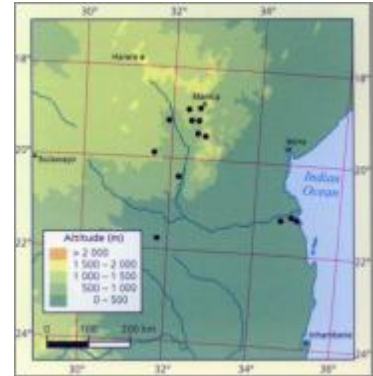


Fig. 10.153. Distribution of *Orbea umbracula*.

base with 2 divergent ridges fused to lateral margins of outer lobes, yellow spotted with red or brown (brown dorsally near base).

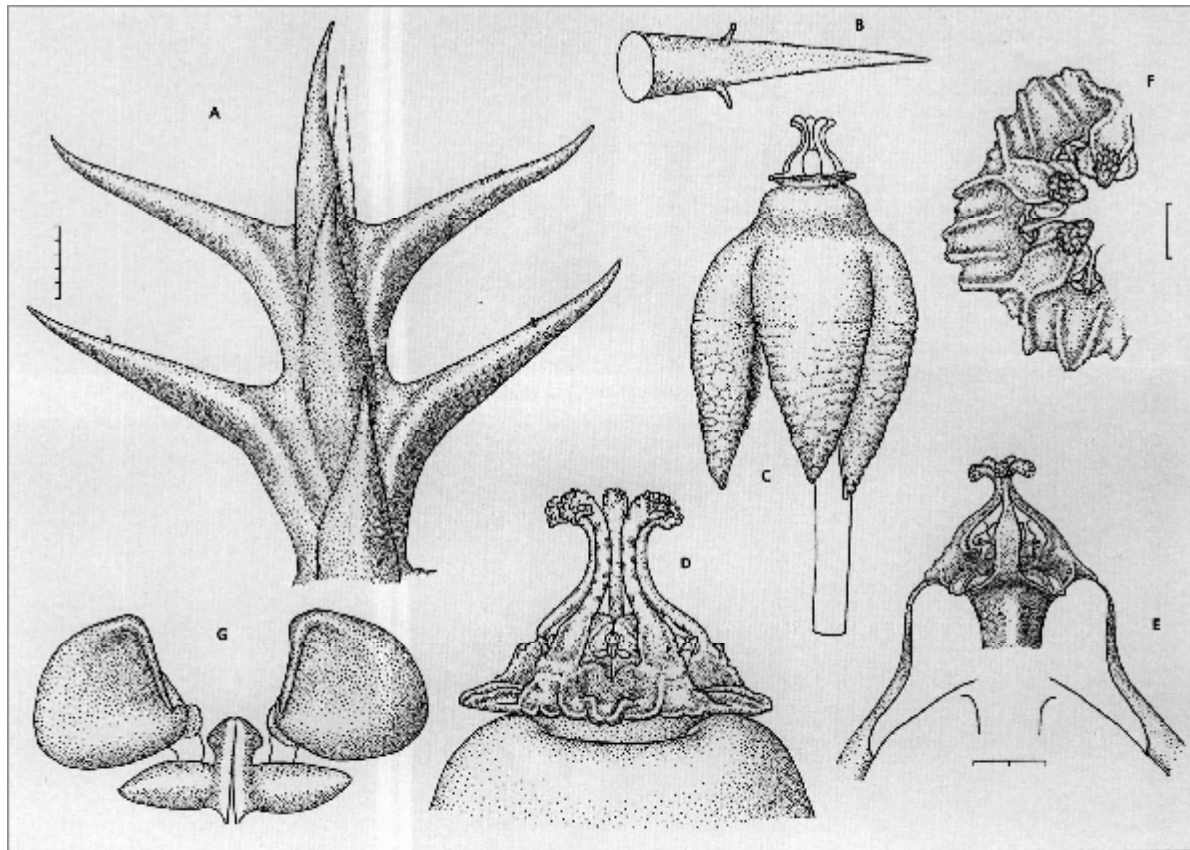


Fig. 10.154. *Orbea umbracula*. A, apex of stem. B, apex of tubercle with stipular denticles. C, side view of flower. D, side view of gynostegium. E, side view of centre of dissected flower. F, face view of part of gynostegium. G, pollinarium. Scale bars: A, C, 5 mm (at A); B, E, 2 mm (at E); D, F, 1 mm (at F); G, 0.25 mm (at E). Drawn from: A, C, D, F, G, PVB 7418, 20 km south of Mutare, Zimbabwe; B, E, PVB 7405, south of Save River, Sofala Province, Mozambique.

Distribution and habitat

Orbea umbracula is now quite well known from the relatively low-lying region between Moodies Pass, Mutare and Gonarezhou in the eastern to south-eastern corner of Zimbabwe. These localities are all to some extent associated with the drainage system of the Save or Sabi River. It is also known from several collections in Moçambique in the area around the mouth of the Save River. Some of these are within 3 km of the coast and they lie about 200 km to the east of the Zimbabwe localities. It remains unknown whether it occurs in the intervening territory.

In Zimbabwe this species seems generally to occur on pale, sandy soils in open *Brachystegia* woodland. In Moçambique plants were found in one spot in a *Baikaea* (Rhodesian teak) forest with lots of leaf-litter, and in two others they were growing among leaf-litter, dead twigs and clumps of small grasses on the edge of 'for-est islands' mainly consisting of *Androstachys johnsonii*, the Lebombo ironwood.

Diagnostic features and relationships

Plants of *O. umbracula* form small clumps, mostly with erect stems but occasionally with a few stems spreading beneath the soil. With their long, slender, tapering tubercles up to 20 mm long, the stems are similar to those of *O. caudata*, *O. rogersii* and *O. tapscottii*. They always seem to be greyish and are usually mottled and lined with purple. Although they look quite spiky, the tubercles are soft and they have the effect of breaking up the outline of the plant to make it more inconspicuous. A little distance from their tip, there are two small, erect, almost cylindrical stipular denticles and these indicate that the remainder of the tubercle is actually made up of the leaf-rudiment, which is otherwise indistinguishable from the rest of the tubercle. With time this leaf-rudiment shrivels and wears off.

The manner in which the flower is held in *O. umbracula* is particularly unusual. Inflorescences mostly arise below the middle of the stem, though often well above the base and, with time, a thick peduncle develops. The pedicels, which are extremely variable in length even on one inflorescence, are often erect and hold the flower up among the tips of the stems or even above them.

In this species the flowers are about 40 mm across when fully spread out but usually their lobes are strongly reflexed. This habit pushes the annulus and corona more to the fore and makes the flower appear much smaller than it really is. Not particularly pretty, it has a brownish red colour (often 'liver-coloured', as it was originally and very aptly described), usually with an irregular reticulation of yellow spots on the lobes, though they may also be plain



Fig. 10.155. *O. umbracula*, PVB 7680, south of Mambone, Inhambane Province, Mocambique.

brown. From the middle outwards the lobes are transversely rugulose and shiny and they have a fringe of small, fixed cilia along most of their margins. Towards the centre and on the annulus the inside of the flower is smooth and dull, i.e. not at all shiny. The annulus rises steeply in the centre to form a small column and in so doing produces the small tube which surrounds the base of the gynostegium. A slight, unpleasant odour is given off by the flowers.

The outer corona lobes are short and dark brown but nevertheless match the colour of the annulus, spreading out above it just beyond the mouth of the tube. The inner lobes, which become slender above and rise quite high above the anthers to end in small, thickened and tuberculate tips, are contrastingly yellow sparsely spotted with brown.

Orbea umbracula shares many features

with the South African *O. woodii*, the Mocambican *O. halipedicola* and *O. semota* from East Africa. From *O. woodii* and *O. semota* it is separated by the manner in which the flowers are produced above the stems and by the much longer and swollen-tipped inner corona lobes. *Orbea umbracula* has now been found growing within 60km of extensive populations of *O. halipedicola*, from which it is easily recognisable even when not in flower by the different colour of the stems with their long, tapering tubercles and small, erect, cylindrical stipular denticles. In *O. halipedicola* the tubercles are tipped with a shorter, more flattened tooth and the denticles merge into and run along the side of this tooth for a short distance. Furthermore, in *O. halipedicola* the corolla lobes are less strongly reflexed, the annulus is much broader and flatter, it is constricted towards the base and, fur-



Fig. 10.156. *O. umbracula*, PVB 7405, south of Save River, Sofala Province, Moçambique.

ORBEA ROGERSII



Fig. 10.157. *O. umbracula*, Peckover, near Chipinga, Zimbabwe, short-pedicelled flower.

thermore, the margins of the lobes are fringed with vibratile cilia. Leach mentioned that the flowers were humifuse in *O. halipedicola* and possessed longer pedicels but in fact the flowers in this species are not usually pressed to the ground and may have pedicels as little as 15 mm long, whereas they may be up to 40 mm long in *O. umbracula*.

History

Orbea umbracula was first gathered in March 1943 by a Mr. Whittall, along the Turgwe River south of Birchenough Bridge. Material was collected in 1954 by Emden A. Pienaar and in 1956 he took Leach to the locality where he had found it, which was at Moodies Pass, a little east of Bikita, in south-eastern Zimbabwe. From the collection that was then made, material was sent to Pretoria where it was cultivated and described somewhat later. It has generally been considered to be endemic to Zimbabwe (Leach 1978a: 45). Only in December 1997 was it first recorded outside Zimbabwe by the present author in the coastal parts of Mocambique, where further records were made in December 1998.



Fig. 10.158. *O. umbracula*, Peckover, near Chipinga, Zimbabwe. Flowers with especially long pedicels.

23. *Orbea rogersii*

Orbea rogersii (L.Bolus) Bruyns, *Aloe* 37: 76 (2001).
Stapelia rogersii L.Bolus, *Ann. Bot. Herb.* 1:194 (1915).

Caralluma rogersii (L.Bolus) E.A.Bruce & R.A.Dyer, *Bull. Misc. Inform.* 1934: 303 (1934).

Pachycymbium rogersii (L.Bolus) M.G.Gilbert, *Bradleya* 8: 28 (1990).

Angolluma rogersii (L.Bolus) Plowes, *Excelsa* 16:120 (1994).

Type: Botswana, Mahalapye, Rogers 6298 (BOL).

Usually small succulent forming clump 60-500 mm diam., not rhizomatous. Stems 30-100 mm long, 8-10 mm thick (excluding teeth), slender, erect, pale green to grey-green flecked with red-brown; *tubercles* 10-20 mm long, arranged loosely into 4 obtuse rows along stem with slight groove between rows, tapering into slender conical ascending to spreading acuminate tooth with pair of small denticles near apex. *Inflorescences* 1-8 per stem mainly in upper half, each of 1-3 (-8) flowers developing in gradual (to rapid) succession from swollen peduncular patch (< 5 mm long); *pedicel* 8-15 mm long, 1.5 mm thick, ascending, with few deltoid bracts 1-2 mm long at base; *sepals* 3-4 mm long, 1.0-1.5 mm broad at base, lanceolate,



Fig. 10.159. *O. rogersii*, PVB 6507, north-west of Makwee, Botswana.

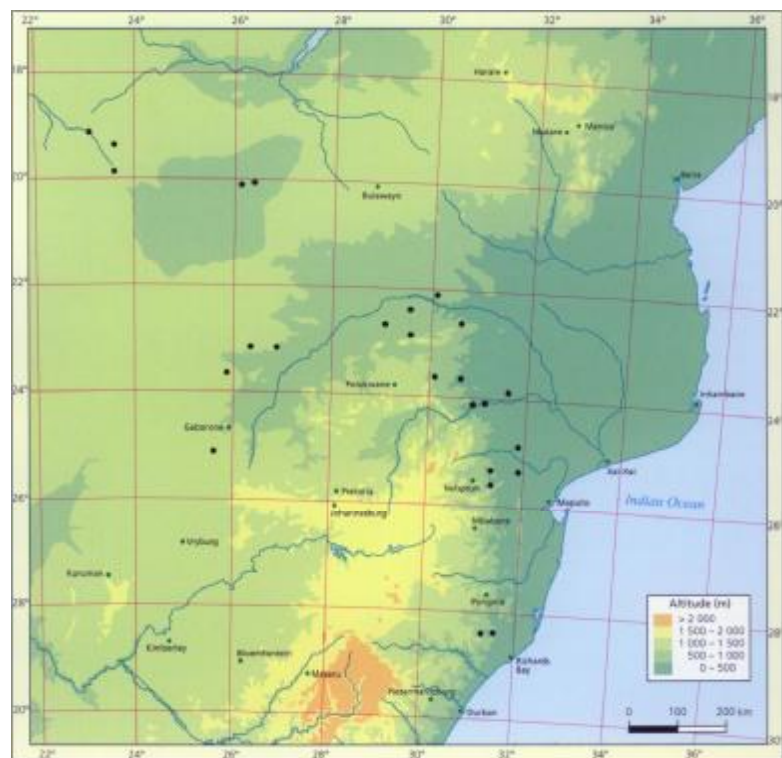


Fig. 10.160. Distribution of *Orbea rogersii*.

acuminate. *Corolla* 25-35 mm diam., rarely expanding fully, very deeply and narrowly lobed; outside smooth pale green with few radial darker veins; inside finely papillate on lobes but with cylindrical papillae (up to 0.5 mm long) on swollen 'annulus', pale greenish yellow to white on united portion; *tube* $\pm$ 0.5-1.0 mm deep, very short, formed by abruptly thickened 'annulus' immediately below sinuses of lobes and around base of gynostegium; *lobes* 18-22 mm long, 3-5 mm broad at base, ascending-incurved,

rarely spreading, linear-acute, with margins incurved for lowest 2-4 mm then replicate so inner surface strongly convex except near base, with transparent clavate-globose non-vibratile cilia 1.0-2.5 mm long along lower margins (incurved portions and $\pm$ 1 mm beyond them). *Corona* $\pm$ 8-10 mm tall, 5 mm broad, raised above tube on stout $\pm$ cylindrical stipe 1 mm long, cream; *outer lobes* 1.5-3.0 mm long, $\pm$ 0.75 mm broad, spreading in lower half then slightly ascending, narrowly rectangular to lanceolate,

1-3-toothed at apex, margin somewhat raised in lower third so lobe channelled there; *inner lobes* 8-10 mm long, dorsiventrally flattened and adpressed to backs of anthers for lower half of anthers then bifid (occasionally trifid) into slender terete filiform lobules 7-9 mm long twisted together and entangled towards apices, with similarly filiform and long dorsal appendage arising near base and initially laterally flattened then terete (often with 1-3 further small dorsal horns).

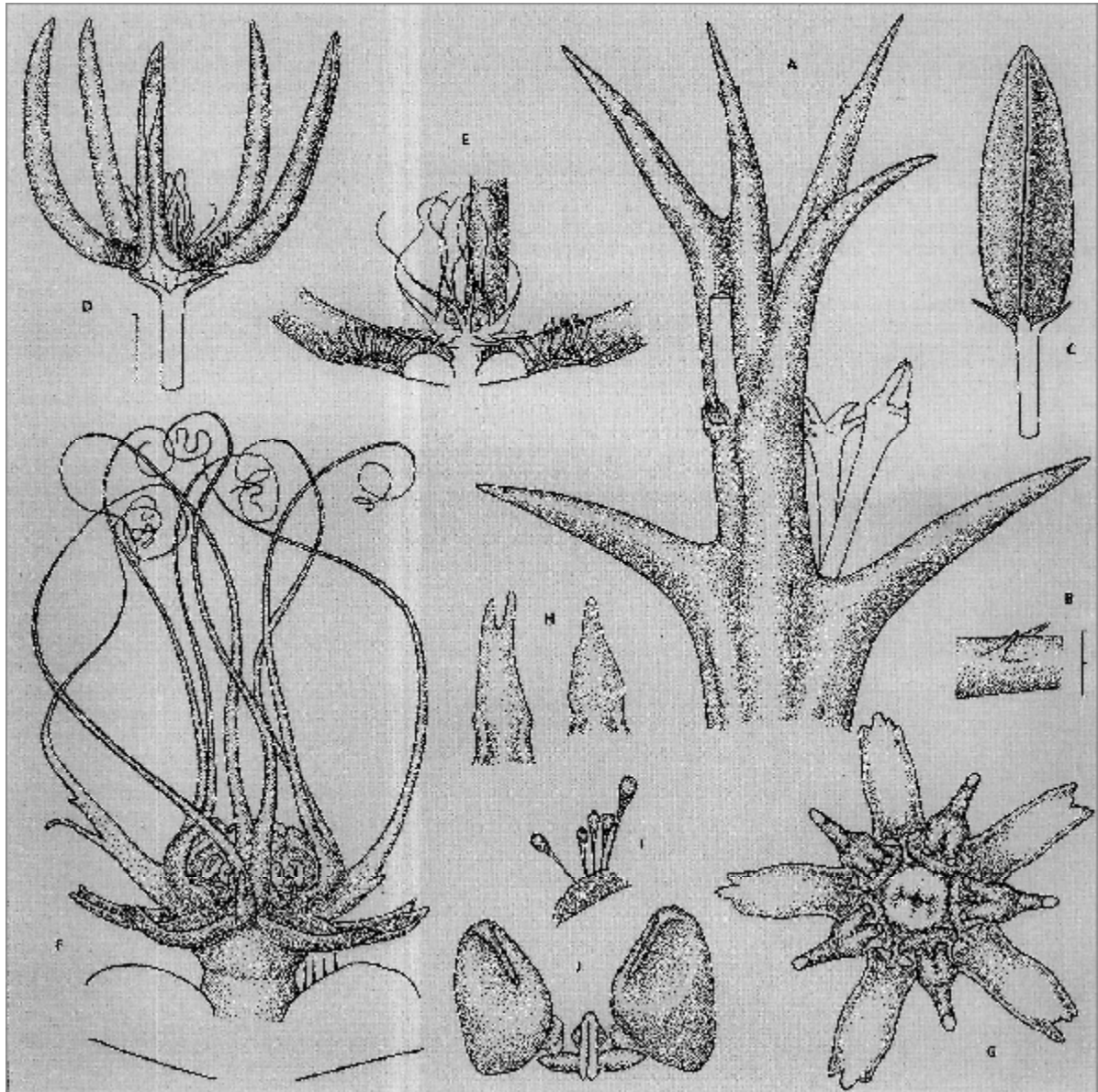


Fig. 10.161. *Orbea rogersii*. A, apex of stem. B, part of tubercle with stipular denticles. C, bud. D, side view of flower. E, side view of centre of dissected flower. F, side view of gynostegium. G, face view of gynostegium with long inner lobules excised. H, face view of outer corona lobe. I, marginal cilia near base of corolla lobe. J, pollinarium. Scale bars: A, C, D, 5 mm (at D); B, 2 mm; E, 3 mm (at B); F, G, H, I, 1 mm (at B); J, 0.25 mm (at B). Drawn from: A, C, D, PVB 4473, near Alldays; B, E, F, G, H (right hand), I, J, PVB 6507, north-west of Makwee, Botswana; H (left hand), PVB 6504, north of Maun, Botswana.

Distribution and habitat

Orbea rogersii is widely distributed but has been very scantily recorded. In Botswana it is found north of Maun on the southern edge of the Okavango Delta and then in the east from around Nata southwards to near Lobatse (Hargreaves 1997). In Zimbabwe it is recorded only in the low-lying, hot and relatively dry country in the south near Beit Bridge and in the south-eastern corner of the country in the lower Sabi Valley. In South Africa there are very few records. Here it occurs in the region north of the Soutpansberg and in the Lowveld further south-east bordering on and inside the Kruger National Park. It is also known in KwaZulu-Natal from the vicinity of Ulundi and from Swaziland.

Plants are generally scattered, rarely locally common, and usually grow in flat, sandy areas around the foot of a tree (often species of *Acacia* or *Colophospermum mopane*) or inside a small shrub.

Diagnostic features and relationships

Specimens of *O. rogersii* often become large (up to 500 mm in diameter), with the stems very densely and tightly packed into a clump but they do not have any tendency to spread underground. The stems are slender and have long, slender, ascending teeth along them which break up their outline. They are attractively mottled with red-brown.

Flowers are borne in many small inflorescences along the stems, mainly towards their apices. Each inflorescence gives rise to a small, persistent, slightly projecting 'peduncular patch' and the presence of many of these on each stem is one of the ways of recognising this



Fig. 10.162. *O. rogersii*, PVB 6507, north-west of Makwee, Botswana.

species even when it is without flowers. Usually when the plant comes into bloom, large numbers of flowers open all over it almost simultaneously (one from each of many of the inflorescences) and thus cover it. They have unusually long, narrow, pentagonal buds whose edges are somewhat undulating around the middle, though all traces of these undulations disappear once the flower opens. The medium-sized flowers always face upwards but intermingle with the stems. They are a dull yellow, becoming whitish towards the centre, and have narrow lobes with only a small united area in the centre around the corona. They emit a weak smell of decaying fruit. For most of their length the lobes are strongly convex above, with their margins folded right back out of sight. Near the base, the margins fold upwards and here they are adorned with a row of remarkable cilia. These are altogether transparent, with an almost spherical, shiny apex which tapers suddenly into a very slender stem. They are fairly rigidly fixed (and so are not at all vibratile) and most of them are held facing upwards so as to form a dense cluster at the sinuses of the lobes. The small, central area around the corona is much thickened and covered with cylindrical,

hair-like papillae and this 'mini-annulus' gives rise to a very small tube around the base of the gynostegium.

The corona is raised somewhat out of the tube so that the outer lobes spread out and touch the corolla below the bases of the lobes and between the patches of cilia. The whole structure is a very pale cream, slightly paler than the centre of the corolla, and contrasts strongly with the dark brown pollinia which, consequently, can easily be seen next to the anthers. The simple outer lobes, which have an unusually thin texture, are channelled above towards their bases and joined to the inner only at their bases. It was because of this that Mrs. Bolus originally placed the species in *Stapelia* and not in *Caralluma*. The lobes are particularly variable in the shape of their apices. The inner ones are dorsiventrally flattened and adpressed to the anthers lower down but then they divide into two (or three) very long, slender and filiform lobules which rise up and become intertwined in the centre. The dorsal projection is laterally flattened towards its base (sometimes with a few small dorsal horns in this part) and then becomes similarly long, slender and filiform to join the general confusion of fine, intertwined, filiform lobules in the centre.

Such a profusion of hairs and long thin lobes in the centre of the flower is unique. However, since many of the species of *Orbea* have a dense crust of hairs on the corolla around the corona and also bear cilia along the margins of the lobes, none of the coralline hairs in *O. rogersii* should come as a surprise. Nevertheless, the shape of the inner corona is without precedent, although the dorsiventral and lateral flattening towards their bases show that these are much modified from the usual structures. Molecular data suggest that *O. paradoxa*, *O. rogersii* and *O. semota* are related, but this requires further investigation.

History

Orbea rogersii was discovered by the missionary and prolific botanical collector Frederic A. Rogers at Mahalapye in eastern Botswana in 1914 and he seems to have found it in March 1914 at Lobatse as well. It was described by L. Bolus as *Stapelia rogersii* from plants from Mahalapye that were cultivated at Kirstenbosch. This species has been recorded very few times in Zimbabwe. The first recorded collection from there was made by Frederick Eyles and Louis Vereker in January 1934 (K, SRGH records) and the only other collection is one made by L.C. Leach east of Beit Bridge, which flowered in 1961. It is similarly rare in KwaZulu-Natal where it has been recorded only twice: once by F.J. Gerstner in January 1940 and more recently by Dennis de Kock in 1981. Both of these collections were made near Ulundi.



Fig. 10.163. *O. rogersii*, PVB 6434, south of Shoshong, Botswana. A robust specimen about 300 mm broad at the base of a small shrub of *Acacia tortilis*, in habitat, December 1995.

24. *Orbea pulchella*

Orbea pulchella (Masson) L.C. Leach, *Kirkia* 10: 290 (1975).

Stapelia pulchella Masson, *Stap. Nov.*: 22, t. 36 (1797).
Podanthes pulchella (Masson) Haw., *Syn. Pl. Succ.*:

33 (1812).

Type: South Africa, Masson (missing).

Lectotype: Masson, *Stap. Nov.*: t. 36.

Dwarf succulent forming clump 50-300 mm diam, not rhizomatous. Stems 25-100 mm long, 5-10 mm thick (excluding teeth), (shortly) decumbent, green mottled with purple-brown; *tubercles* 4-9 mm long, arranged loosely into 4 obtuse rows along stem with groove between rows, tapering into spreading to ascending conical acute tooth (usually lacking denticles). *Inflorescence* 1 per stem, of 1-3 flowers developing successively from short peduncle < 5 mm long, with few small bracts < 1.5 mm long; *pedicel* 10-30 mm long, 2 mm thick, horizontal to ascending usually with ascending apex; *sepals* 4-10 mm long, 2 mm broad at base, ovate-lanceolate, acuminate. *Corolla* 30-55 mm diam., rotate to shallowly bowl-shaped; outside smooth, pale green towards base, flecked and veined with purple-brown on lobes; inside pale yellow with purple-brown to red spots becoming smaller and denser on annulus, uniformly purple-brown or red around and beneath gynostegium, transversely papillate-rugulose except towards base of tube; tube shallowly bowl-shaped, containing and often formed by thickened pentagonal (with corners below sinuses of lobes) sometimes very obscure annulus 1.5-2.0 mm thick and $\pm$ 10-12 mm diam., with ring of cylindrical bristles in base immediately around gynostegium; *lobes* 13-20 mm long, 12-16 mm broad at base, spreading to recurved, deltate to deltate-ovate, very acute or acuminate, margins ciliate. *Corona* $\pm$ 5 mm tall, 6-7 mm broad, raised above base of tube on stout cylindrical stipe $\pm$ 1 mm tall; *outer lobes* 2-3 mm long, ascending, deeply channelled on upper surface, $\pm$ rectangular, truncate to shallowly apically notched, laterally fused towards base to lower rear of inner lobes, dark purple-red; *inner lobes* $\pm$ 3 mm long, adpressed to backs of anthers and exceeding them to rise in small column in centre then slightly diverging, dorsiventrally flattened below becoming terete near apex, usually with deltoid to truncate often transversally flattened dorsal projection near base.



Fig. 10.164. *O. pulchella*, PVB 4262, Humewood, Port Elizabeth, in habitat, April 1990.

Distribution and habitat

Orbea pulchella is best known from around Port Elizabeth, with a single record from the Baviaanskloof and another from Carlisle Bridge to the north-east (Leach 1978a). It occurs more or less in an area where the distributions of *O. variegata* and *O. verrucosa* overlap, although neither of these species ever seems to have been recorded in the area around Port Elizabeth, where *O. pulchella* is most prevalent.

Diagnostic features and relationships

The plant and the corolla of *O. pulchella* are more or less indistinguishable from those of *O. verrucosa*. In particular, in *O. pulchella* the corolla is finely spotted on a cream-yellow background and it has a small annulus rising out of the side of the tube just as in *O. verrucosa*.

From *O. verrucosa*, *O. pulchella* differs chiefly in characters of the corona. The outer

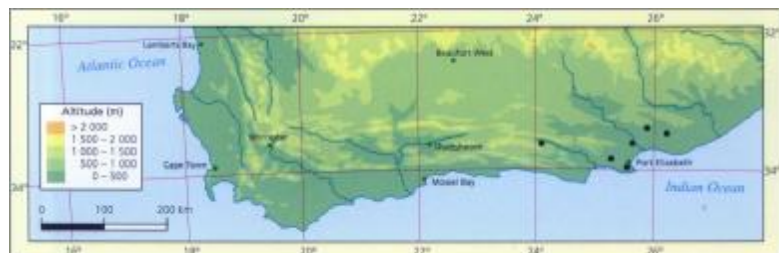


Fig. 10.165. Distribution of *Orbea pulchella*.

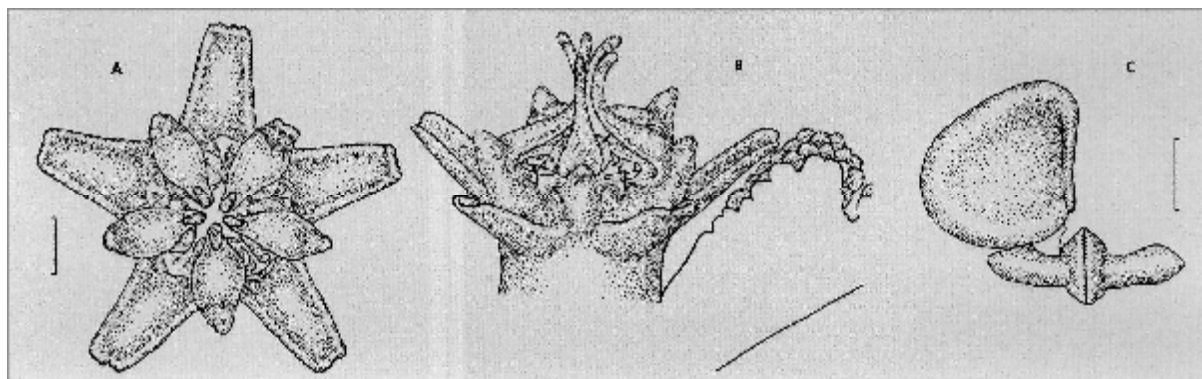


Fig. 10.166. *Orbea pulchella*. A, face view of gynostegium. B, side view of gynostegium. C, part of pollinarium. Scale bars: A, B, 1 mm (at A); C, 0.25 mm. Drawn from: PVB 4262, Humewood, Port Elizabeth.

ORBEA VERRUCOSA



Fig. 10.167. *O. pulchella*, PVB 4262, Humewood, Port Elizabeth, flower with prominent annulus.

lobes are considerably longer than in *O. verrucosa* and become slightly narrower towards their truncate ends. The inner lobes are longer as well and rise in a small column in the centre. They have a noticeable dorsal ridge near their base.

The peculiar distribution of this species in the area where *O. variegata* and *O. verrucosa* overlap suggests that it might be a hybrid between the two of them. Pollination experiments have shown that direct crosses of *O. variegata* and *O. verrucosa* all had much larger annuli and were far more coarsely mottled than in *O. pulchella*, so further crossing might be necessary to produce something more like *O. pulchella*. In the differences in the corona, the flower is intermediate between the two of them. However, where it occurs around Port Elizabeth, one only finds *O. pulchella* and this

suggests that, if it were of hybrid origin, it has managed to establish itself as a viable breeding species.

History

This species was also discovered by Francis Masson and flowered at Cape Town in his garden in 1793. He did not intimate where he had obtained material but it is reasonable to assume that it was from somewhere in the area around the present-day Port Elizabeth.

Masson's illustration is not particularly clear and this name has come to be associated with material collected around Port Elizabeth largely because of the interpretation placed on it by N.E. Brown (1907-09). In this case (unlike that of *O. verrucosa*) no type has been found to clarify the position.



Fig. 10.168. *O. pulchella*, PVB 4262, Humewood, Port Elizabeth, flower with hardly any annulus visible.

25. *Orbea verrucosa*

Orbea verrucosa (Masson) L.C.Leach, *Kirkia* 10: 290 (1975).

Stapelia verrucosa Masson, *Stap. Nov.*: 11, t. 8 (1796).

Podanthes verrucosa (Masson) Haw., *Syn. Pl. Succ.*: 33 (1812).

Type: South Africa, Cape, in dry places, Masson (BM).

Stapelia irrorata Masson, *Stap. Nov.*: 12, t. 9 (1796).

Podanthes irrorata (Masson) Haw., *Syn. Pl. Succ.*: 33 (1812).

Orbea irrorata (Masson) L.C.Leach, *Excelsa Taxon. Ser.* 1:27 (1978).

Type: South Africa, Cape, Masson (missing).

Lectotype: Masson, *Stap. Nov.*: t. 9.

Stapelia roriflua Jacq., *Stap.*: 119 (1806-19).

Podanthes roriflua (Jacq.) Sweet, *Hort. Brit.*, ed. 1:278 (1826).

Piранthus rorifluus (Jacq.) Decne. in DC, *Prodr.* 8: 664 (1844).

Stapelia verrucosa var. *roriflua* (Jacq.) N.E. Br., *Fl. Cap.* 4 (1): 988 (1909).

Lectotype: Jacq., *Stap.*: t. 19.

Stapelia rugosa J.C.Wendl., *Coll. Pl.* 2: 41, t. 52 (1809) non J.Donn ex Jacq. (1806-19).

Type: none located in Wendlan Herbarium (GOET).

Lectotype: J.C. Wendl., *Coll. Pl.* 2: t. 52.

Podanthes pulchra Haw., *Syn. Pl. Succ.*: 32 (1812).

Stapelia pulchra (Haw.) Schult. in Roem. & Schult., *Syst. Veg.* 6: 28 (1820).

Stapelia verrucosa var. *pulchra* (Haw.) N.E. Br., *Fl. Cap.* 4(1): 987 (1909).

Type: material in cultivation (missing).

Stapelia wendlandiana Schult. in Roem. & Schult., *Syst. Veg.* 6: 39 (1820).

Orbea wendlandiana (Schult.) Schult. in Roem. & Schult., *Syst. Veg.* 6: 834 (1820).

Lectotype: J.C.Wendl., *Coll. Pl.* 2: t. 52 (1809).

Podanthes pulchra var. *major* Sweet, *Hort. Brit.*, ed. 1:278 (1826).

Type: *Bot. Mag.* 20: t. 786 (1804).

Podanthes pulchra var. *verrucosa* G.Don, *Gen. Hist.* 4: 118 (1837-8), nom. *superfl.*

Type: *Bot. Mag.* 20: t. 786 (1804).

Stapelia fucosa N.E. Br., *Fl. Cap.* 4 (1): 977 (1909).

Orbea verrucosa var. *fucosa* (N.E. Br.) L.C.Leach, *Excelsa Taxon. Ser.* 1: 25 (1978).

Stapelia verrucosa var. *fucosa* (N.E. Br.) P.V.Heath, *Calyx* 1:16 (1992).

Type: Eastern Cape, just south-east of Mt Ayliff, June 1903, N.S. Pillans 173 (BOL).

Stapelia verrucosa var. *conspicua* N.E. Br., *Fl. Cap.* 4 (1): 988 (1909).

Type: Eastern Cape, Glen Avon Estate, June 1903, N.S. Pillans 192 (BOL).

Stapelia verrucosa var. *pallenscens* N.E. Br., *Fl. Cap.* 4 (1): 988 (1909).

Type: Eastern Cape, Glen Avon Estate, July 1903,
N.S. Pillans 56 (BOL).

Stapelia verrucosa var. *punctifera* N.E. Br., Fl. Cap.
4 (1): 988 (1909).

Lectotype: Eastern Cape, Bellevue, Alexandria
distr., 1904, Brocklebank sub N.S. Pillans 655
(BOL).

Stapelia verrucosa var. *robusta* N.E. Br., Fl. Cap. 4 (1):
988 (1909).

Type: Eastern Cape, Glen Avon Estate, July 1903,
N.S. Pillans 604 (BOL).

Dwarf succulent forming clump 50-300 mm diam, not rhizomatous. Stems 25-100 mm long, 5-10 mm thick (excluding teeth), (shortly) decumbent, green mottled with purple-brown; tubercles 4-9 mm long, arranged loosely into 4 obtuse rows along stem with groove between rows, tapering into spreading to ascending conical acute tooth (usually lacking denticles). Inflorescence 1 per stem, of 1-3 flowers developing successively from short peduncle mostly < 5 mm long, with few small bracts < 1.5 mm long; pedicel 10-30 mm long, 2 mm thick, horizontal to ascending usually with ascending apex; sepals 4-10 mm long, 2 mm broad at base, ovate-lanceolate, acuminate. Corolla 45-60 mm diam, rotate to shallowly bowl-shaped often with flat base; outside smooth, pale green towards base, flecked and veined with purple-brown on lobes; inside pale yellow with purple-brown to red spots, the spots becoming smaller and denser on annulus, uniformly purple-brown or red around and beneath gynostegium, transversely papillate-rugulose except towards base of tube; tube shallowly bowl-shaped, containing and often formed by thickened pentagonal (with corners below sinuses of lobes)

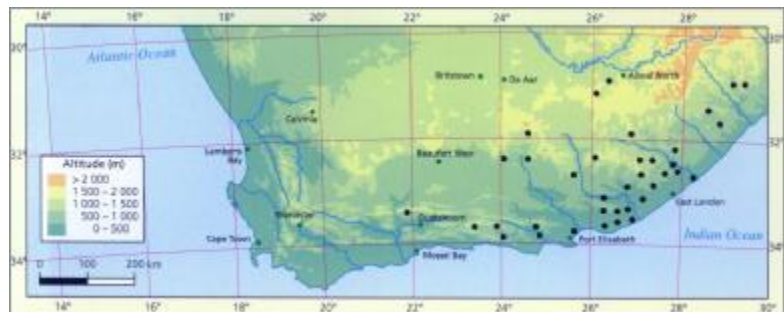


Fig. 10.169. Distribution of *Orbea verrucosa*.

sometimes very obscure annulus 1.5-2.0 mm thick and $\pm$ 10-12 mm diam., with ring of cylindrical bristles in base immediately around gynostegium; lobes 13-20 mm long, 12-16 mm broad at base, spreading to recurved, deltate to deltate-ovate, very acute or acuminate, margins eciliate. Corona $\pm$ 4 mm tall, 6-7 mm broad, raised above base of tube on stout cylindrical stipe $\pm$ 1 mm tall; outer lobes 1-2 mm long, horizontally spreading to slightly deflexed, deeply channelled on upper surface, with shallow to deep triangular notch in apex dividing lobe into 2 deltoid slightly ascending lobules towards apex, laterally fused towards base to lower rear of inner lobes, dark purple-red; inner lobes 1.0-1.5 mm long, adpressed to backs of anthers and equalling to exceeding them, sometimes meeting in centre and with upturned apices, dorsiventrally flattened and narrowly deltoid, slightly gibbous on rear towards base, rear and margins purple-red, upper surface bright yellow.



Fig. 10.170. *O. verrucosa*, PVB 5388, Inversomo, Kei River Gorge.

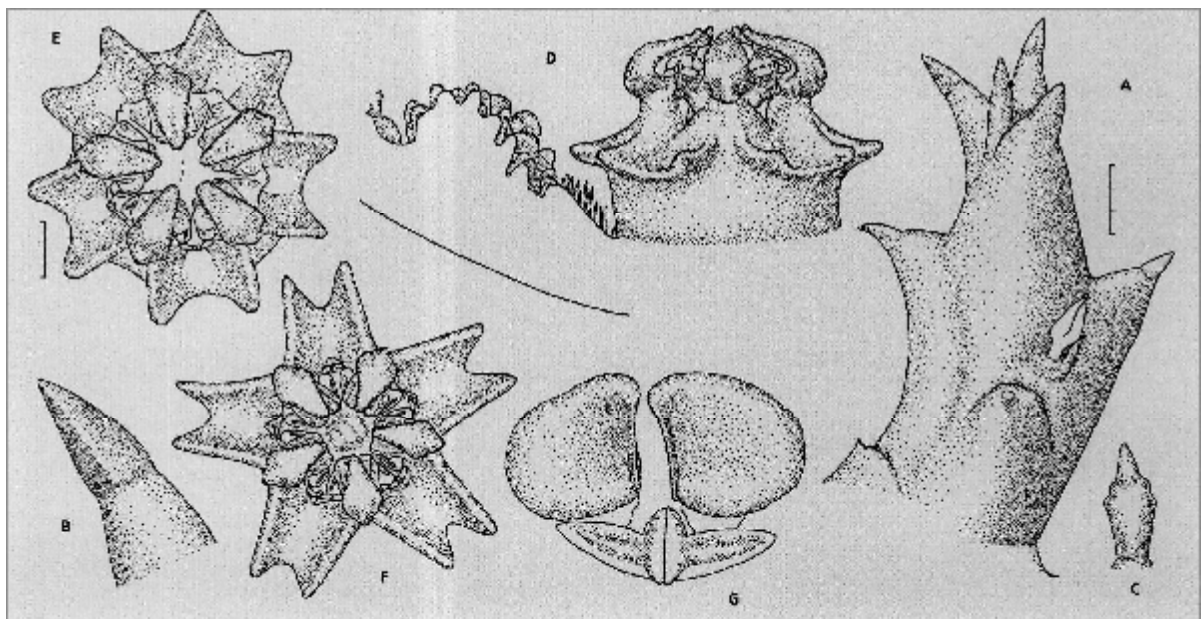


Fig. 10.171. *Orbea verrucosa*. A, apex of stem. B, apex of tubercle. C, bract from inflorescence. D, side view of centre of dissected flower. E, F, face view of gynostegium. G, pollinarium. Scale bars: A, 3 mm; B, C, 1 mm (at A); D-F, 1 mm (at E); G, 0.25 mm (at A). Drawn from: F, PVB 6242, west of Swartberg Pass; rest, PVB 3066, Kamdebooiberg, north of Aberdeen.

Distribution and habitat

Although less well known than *O. variegata*, *O. verrucosa* is also widely distributed and quite common in some areas. It is most common in the Eastern Cape from Port Elizabeth eastwards to the Kei River but it also occurs as far west as Oudtshoorn. In the Great Karoo it is known around Graaff-Reinet and Somerset East, from where it extends north-eastwards as far as near Aliwal North, Mount Frere and Mount Ayliff in the former Transkei.

Plants usually grow on shale banks, or among rocks and small bushes on dry slopes or flats.

Diagnostic features and relationships

In *O. verrucosa* the stems form clumps which sometimes become large and very densely packed but are often small (< 100 mm in diameter) and quite inconspicuous. They are usually green with a weak to bold purple mottling and with relatively small tubercles which are loosely arranged into four rows. Although the stems are less brightly coloured, usually also smaller and with smaller tubercles than those of *O. variegata*, they are otherwise indistinguishable from them.

Inside, the flowers are pale yellow and variously, but usually quite finely, spotted with purple-brown. The dark colour generally becomes concentrated towards the centre which is then darker than the rest. The flower is usually shallowly bowl-shaped, less commonly quite flat, and the inside is covered all over with transverse papillate rugosities. Near the centre there is a small annulus, occasionally barely distinguishable from the surrounding tissue but usually raised up to 2 mm out of the



Fig. 10.172. *O. verrucosa*, PVB 5388, Inversomo, Kei River Gorge.



Fig. 10.173. *O. verrucosa*, PVB 6242, west of Swartberg Pass.

surface. This annulus forms the beginnings of the slightly steeper lower part of the tube and, on the inside, it is often distinctly pentagonal. The tissue of the corolla is somewhat swollen behind the outer corona lobes and thinner between them (i.e. below the sinuses of the corolla lobes) so that five grooves arise in the lower part of the tube alternating with the outer corona lobes. In live flowers these grooves may be accentuated by being slightly darker but they may also be absent altogether and the lower part of the tube is then circular. Towards the base of the tube the rugosities give way to a dense crust of small cylindrical hairs (fig. 29 G).

In this species the corona consists of dark purple-red outer lobes which spread outwards and are often very short and channelled deeply on their upper surface. The inner lobes, which are bright yellow with purple-red margins, are adpressed to the anthers but they do not rise above the anthers in the centre and have at most a very small dorsal swelling near the base.



Fig. 10.174. *O. verrucosa*, PVB 7094, near Kareedouw.

Orbea verrucosa is in many ways similar to *O. variegata* and very similar indeed to *O. pulchella*. Vegetatively they cannot be separated reliably. Florally *O. verrucosa* and *O. pulchella* are most similar and they differ from *O. variegata* by the much smaller annulus which appears merely as a ridge on the side of the tube and does not itself form the tube around the corona as in *O. variegata*. Among the three species, the corona has the shortest outer lobes and the shortest inner lobes in *O. verrucosa*.

History

This species was figured for the first time by Francis Masson (1796-8) but he did not say how or where he had obtained his material. Today, it is reasonably well known but not to the same degree as *O. variegata*, despite the fact that they have similarly wide distributions and are both easy to cultivate. Not quite as many variants of *O. verrucosa* have been given varietal or specific names as happened in *O. variegata* but N.E. Brown described several varieties from material collected by N.S. Pillans on the Glen Avon Estate near Somerset East in July 1903. Leach (1978a) abandoned all of these but maintained a 'var. *fucosa*', which had been described as *Stapelia fucosa* by N.E. Brown and was based on material collected in June 1903 by N.S. Pillans in the former Transkei. In var. *fucosa* the stems had shorter tubercles and the flowers are slightly smaller, darker and flatter towards the centre than in var. *verrucosa*. There seems to be no basis for maintaining this variety either and it is not recognised here.

As is often the case, Masson's illustration is not very precise and there have been problems in associating it with known plants. Leach's discovery of a type specimen, that had survived nearly 200 years in alcohol at the British Museum (Leach 1978a) conclusively resolved any doubt surrounding the identity of this species.

26. *Orbea namaquensis*

Orbea namaquensis (N.E. Br.) L.C. Leach, Kirkia 10: 290 (1975).

Stapelia namaquensis N.E. Br., Gard. Chron. N.S. 18: 648 (1882).

Type: South Africa, Cape, Namaqualand, Barkly 64 (K).

Stapelia namaquensis var. *ciliolata* N.E. Br., Gard. Chron. N.S. 18: 648 (1882).

Stapelia ciliolata (N.E. Br.) Rust, Monatsschr. Kakt. 6: 43 (1896).

Type: Cape, Namaqualand, Barkly 38 (K).

Stapelia namaquensis var. *minor* N.E. Br., Gard. Chron. N.S. 18: 648 (1882).

Type: Cape, Namaqualand, Barkly 64 bis (K).

Stapelia namaquensis var. *tridentata* N.E. Br., Gard. Chron. N.S. 18: 648 (1882).

Stapelia tridentata (N.E. Br.) Rust, Monatsschr. Kakt. 6: 43 (1896).

Type: Cape, Namaqualand, Barkly (K).

Stapelia namaquensis var. *bidens* N.E. Br., Fl. Cap. 4 (1): 99 (1909).

Type: Cape, Namaqualand, without precise locality, Bolus (BOL).

Succulent forming clump 50 mm-1 m diam., not rhizomatous. Stems 30-100 mm long, 20-40 mm thick (excluding teeth), stout and often nearly cylindrical, shortly decumbent, green heavily mottled with purple-brown; *tubercles*

4-10 mm long, arranged loosely into 4 very broadly obtuse rows along stem ± without groove between rows, tapering into spreading conical stoutly acute tooth, sometimes with 1 or 2 denticles near apex. *Inflorescence* 1 per stem in lower half, of 1-2 (-4) flowers developing in gradual succession from short peduncle mostly < 10 mm long; *pedicel* 25-40 mm long, 4-5 mm thick, heavily striped with purple-red, spreading with upturned apex holding flower facing upward on ground; *sepals* 6-8 mm long, 3-5 mm broad at base, ovate, acuminate. *Corolla* 70-100 mm diam., rotate; outside smooth, pale green to deeply suffused with purple-brown, with 3-5 longitudinal darker veins running down each lobe and fading towards base of tube; inside rugose with transverse papillate ridges on lobes and around annulus, obscurely rugulose on annulus becoming smooth towards centre, pale greenish yellow to bright yellow variously spotted and lined with purple-brown, bright yellow under annulus and with dark purple-brown ring around base of gynostegium; *tube* very shallowly bowl-shaped and slightly pentagonal, formed around gynostegium by thick (3-4 mm) annulus 8-10 mm tall and recurved so that rim often touches corolla surface outside tube, with narrow ring of cylindrical-acute black bristles in base around gynostegium; *lobes* 25-32 mm long, 20-25 mm broad at base, spreading to recurved, broadly ovate, acuminate, often with dense fringe of short (< 1 mm) clavate rigidly fixed marginal cilia except towards bases and apices. *Corona* ± 8 mm tall, 16 mm broad, raised above base of tube on stout cylindrical often dark purple stipe 1-2 mm long; *outer lobes* 6-8 mm long, 1.5-2.0 mm broad, initially horizontal then ascending, linear or linear-lanceolate, acute, yellow dotted with purple-brown

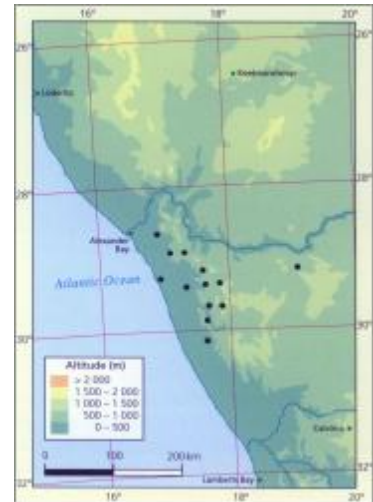


Fig. 10.175. Distribution of *Orbea namaquensis*.

with larger purple-brown patches at base; *inner lobes* 12-15 mm long, adpressed to backs of anthers then slender ± terete connivent-erect with clavate-tuberculate usually recurved tips, with slight rounded dorsal gibbosity at base, yellow dotted with purple-brown.

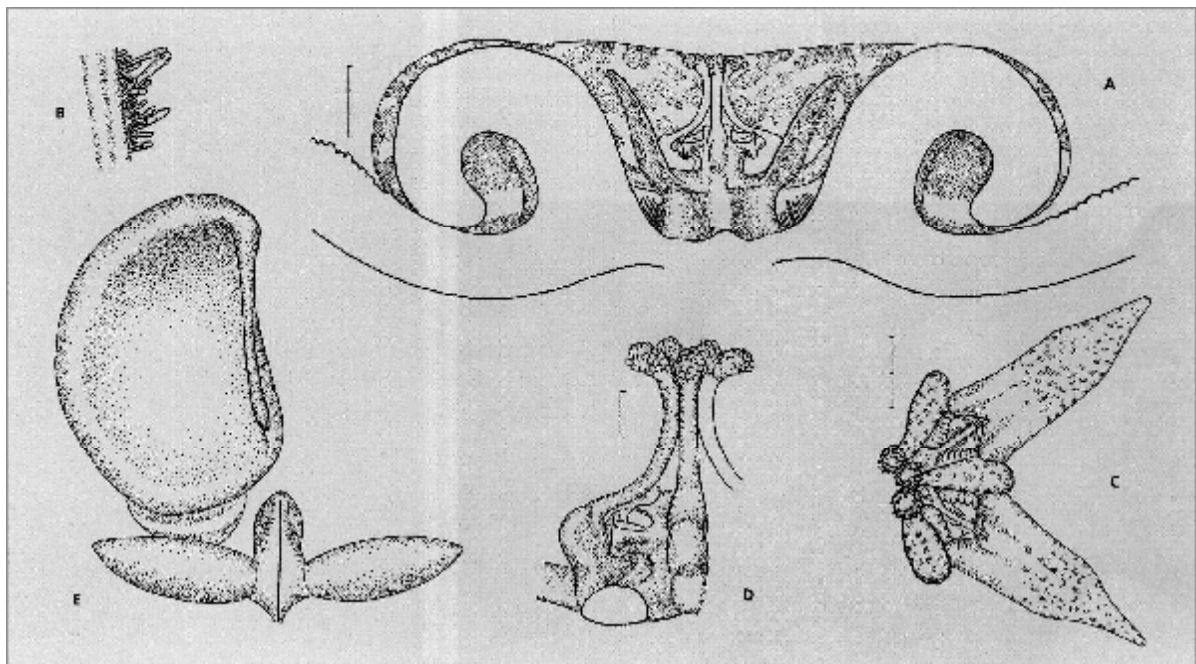


Fig. 10.176. *Orbea namaquensis*. A, side view of centre of dissected flower. B, papillae along margin of lobe around its middle with inside of corolla to right. C, face view of part of gynostegium. D, side view of inner corona lobes. E, pollinarium (one pollinium left out). Scale bars: A, 3 mm; B, 0.5 mm (at A); C, 2 mm; D, 1 mm; E, 0.25 mm (at A). Drawn from: A, D, E, PVB 8253, east of Springbok; B, C, PVB, Brakfontein, Komaggas.

ORBEA NAMAQUENSIS



Fig. 10.177. *O. namaquensis*, PVB 8253, east of Springbok, in habitat, August 2000.



Fig. 10.178. *O. namaquensis*, PVB 8253, east of Springbok, in habitat, August 2000.

Distribution and habitat

Orbea namaquensis is of relatively restricted distribution in Namaqualand and is only known to the south of the Orange River. Below the escarpment, it is found from Doornpoort (a little south of Kubus in the Richtersveld) to near Soebatsfontein. Although I have found it within 10 km of the sea between Port Nolloth and Grootmis, it generally appears to be rare in the coastal *sandveld*. Above the escarpment it is fairly common in the hills from Steinkopf southwards to near the Buffels River, south of Springbok. Further east it rapidly disappears, with a single record from north-east of Concordia and one from Pella, near Pofadder. It seems to be exclusively a species of the arid part of the winter-rainfall area.

Plants of *O. namaquensis* can become extremely common, sometimes growing under almost every bush. Below the escarpment it occurs on gently sloping, usually somewhat gravelly, overgrazed areas. Among the gneiss hills of the Springbok area it often grows in flattish, somewhat disturbed areas under bushes of *Galenia africana* (fig. 64) or *Pteronia incana* or on gravelly slopes.

Diagnostic features and relationships

Specimens of *O. namaquensis* often form large and dense mats up to 1 m or more in diameter. This species has stout stems which, when exposed to enough sunlight, are beautifully marked with purple-brown on green, causing N.E. Brown (1882) to comment that it is 'really handsome, which is saying a great deal for a *Stapelia* plant'. Along the stem are several prominent conical tubercles rather vaguely arranged into four rows. Brown had not, at that stage, seen *O. ciliata* in the live state, whose stems are equally handsome and are, in fact, impossible to separate from those of *O. namaquensis*.

Florally, however, these species are quite different. The flowers of *O. namaquensis* are spotted and lined with purple-brown on yellow and are not uniformly coloured as in *O. ciliata*. They are, in fact, very similar to those of *O. variegata* but are mostly larger and more strikingly marked. As in *O. variegata*, the flower is pressed facing upwards to the ground, and is practically flat. It consists of broadly ovate lobes and a thick annulus near the centre that

forms a bowl-shaped tube around the gynostegium, though this is not as tall as the corona lobes. The annulus curves down towards the corolla and its edge is slightly recurved against the corolla, whereas in *O. variegata* the annulus spreads above the corolla. It is uniformly thick right to this edge, not becoming thin towards the rim as in *O. variegata*, and it forms a small, steep tube in the otherwise almost flat corolla. The surface of the corolla is rugose on the lobes and around the annulus (though not on the area beneath it), but on the annulus itself it is only obscurely rugulose and so it is not nearly as rough there as in *O. variegata*. There are often lots of short, clavate cilia along the margins of the lobes around their middle. In *O. namaquensis* there is also a narrow ring of black cylindrical (here they are sharp-pointed) hairs in the tube formed by the annulus around the base of the gynostegium.

Although somewhat similar to that of *O. variegata*, the corona of *O. namaquensis* shows some obvious differences. The outer lobes taper gradually to a point in their upper half and are not bifid. Initially they spread outwards, after which they ascend and are pressed into the slight corners of the tube formed by the annulus. Their colour matches that of the annulus closely. The inner lobes have clavate-tuberculate apices similar to those in *O. variegata*. They are also connivent in a cluster above the centre of the flower, but they lack any trace of a dorsal horn.

This species has especially large pollinia, the largest in the genus *Orbea* and in fact amongst all the stapeliads.

History

The first recorded collections of *O. namaquensis* were those that were sent to N.E. Brown at Kew in 1874 by Henry Barkly. Brown described the species and three varieties in 1882, adding a fourth in 1909, but these are no longer recognised as distinct (Leach 1978a). Marloth (1932) considered these plants all to belong to *O. variegata* but they do appear to constitute a distinct species.



Fig. 10.179. *O. namaquensis*, PVB, near Komaggas.

27. *Orbea variegata*

Orbea variegata (L.) Haw., *Syn. Pl. Succ.* 40 (1812).
Stapelia variegata L., *Sp. Pl.* 1: 217 (1753).
 Type: South Africa, Cape, Table Mountain, 311/1 (LINN).

Stapelia mixta Masson, *Stap. Nov.* 23, t. 38 (1797).
Orbea mixta (Masson) Haw., *Syn. Pl. Succ.* 38 (1812).
Stapelia variegata var. *mixta* (Masson) N.E. Br., *Fl. Cap.* 4(1): 1000 (1909).
 Type: South Africa, Cape, Masson (missing).
 Lectotype: Masson, *Stap. Nov.*: t. 38.

Stapelia orbicularis Andrews, *Bot. Repos.* 7: t. 439 (1806).

Orbea orbicularis (Andrews) Haw., *Syn. Pl. Succ.* 40 (1812).

Lectotype: *Bot. Repos.*: t. 439.

Stapelia trisulca J.Donn ex Jacq., *Stap.*: t. 33 (1806-19).

Stapelia variegata var. *trisulca* (J.Donn ex Jacq.) N.E. Br., *Fl. Cap.* 4(1): 997 (1909).

Lectotype: Jacq., *Stap.*: t. 33.

Stapelia clypeata J.Donn ex Jacq., *Stap.*: t. 34 (1806-19).

Orbea clypeata (J.Donn ex Jacq.) Haw., *Suppl. Pl. Succ.*: 13 (1819).

Stapelia variegata var. *clypeata* (J.Donn ex Jacq.) N.E. Br., *Fl. Cap.* 4(1): 1000 (1909).

Lectotype: Jacq., *Stap.*: t. 34.

Stapelia bufonia Jacq., *Stap.*: t. 35 (1806-19).

S. variegata var. *bufonia* (Jacq.) N.E. Br., *Hooker's Icon. Pl.* 20: sub. t. 1907 (1890).

Lectotype: Jacq., *Stap.*: t. 35.

Stapelia anguinea Jacq., *Stap.*: t. 37 (1806-19).

Lectotype: Jacq., *Stap.*: t. 37.

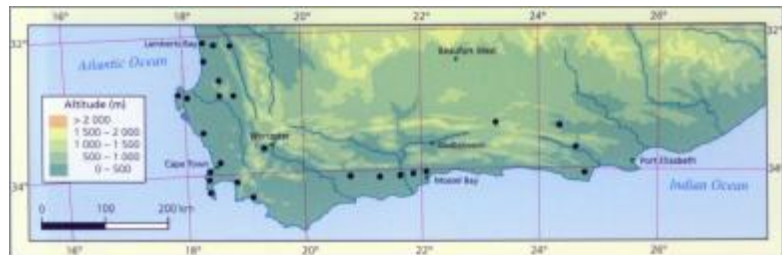


Fig. 10.180. Distribution of *Orbea variegata*.

Stapelia marmorata Jacq., *Stap.*: t. 38 (1806-19).
Orbea marmorata (Jacq.) G.Don, *Gen. Hist.* 4: 120 (1837-8).

Stapelia variegata var. *marmorata* (Jacq.) N.E. Br., *Fl. Cap.* 4(1): 1004 (1909).

Lectotype: Jacq., *Stap.*: t. 38.

Stapelia planiflora Jacq., *Stap.*: t. 40 (1806-19).

Orbea planiflora (Jacq.) Haw., *Suppl. Pl. Succ.*: 12 (1819).

Stapelia variegata var. *planiflora* (Jacq.) N.E. Br., *Fl. Cap.* 4(1): 998 (1909).

Lectotype: Jacq., *Stap.*: t. 40.

Stapelia rugosa J.Donn ex Jacq., *Stap.*: t. 41 (1806-19).

Orbea rugosa (J.Donn ex Jacq.) Sweet, *Hort. Brit.* ed. 1: 277 (1826).

Tridentea rugosa (J.Donn ex Jacq.) G.Don, *Gen. Hist.* 4: 118 (1837-8).

Stapelia variegata var. *rugosa* (J.Donn ex Jacq.) N.E. Br., *Fl. Cap.* 4(1): 1001 (1909).

Lectotype: Jacq., *Stap.*: t. 41.

Stapelia normalis Jacq., *Stap.*: t. 42 (1806-19).

Orbea normalis (Jacq.) G.Don, *Gen. Hist.* 4: 120 (1837-8).

Stapelia variegata var. *normalis* (Jacq.) A.Berger, *Stap. u. Klein.*: 207 (1910).

Lectotype: Jacq., *Stap.*: t. 42.

Stapelia lepida Jacq., *Stap.*: t. 43 (1806-19).

Orbea lepida (Jacq.) L.C. Leach, *Exceisa Taxon. Ser.* 1: 18 (1978).

Lectotype: Jacq., *Stap.*: t. 43.

Stapelia picta J.Donn ex Sims, *Bot. Mag.* 29: t. 1169 (1809).

Orbea picta (Sims) Haw., *Syn. Pl. Succ.* 42 (1812).

Stapelia variegata var. *picta* (Sims) N.E. Br., *Fl. Cap.* 4(1): 1004 (1909).

Lectotype: *Bot. Mag.*: t. 1169.

Stapelia conspurcata Willd., *Enum. Pl.*: 284 (1809).

Orbea conspurcata (Willd.) Sweet, *Hort. Brit.* ed. 1: 277 (1826).

Stapelia variegata var. *conspurcata* (Willd.) N.E. Br., *R. Cap.* 4(1): 1003 (1909).

Type: Cape of Good Hope (B-W 530).

Stapelia planiflora var. *marginata* Willd., *Enum. Pl.*: 284 (1809).

Stapelia marginata (Willd.) Willd., *Enum. Pl. Suppl.*: 13 (1814).

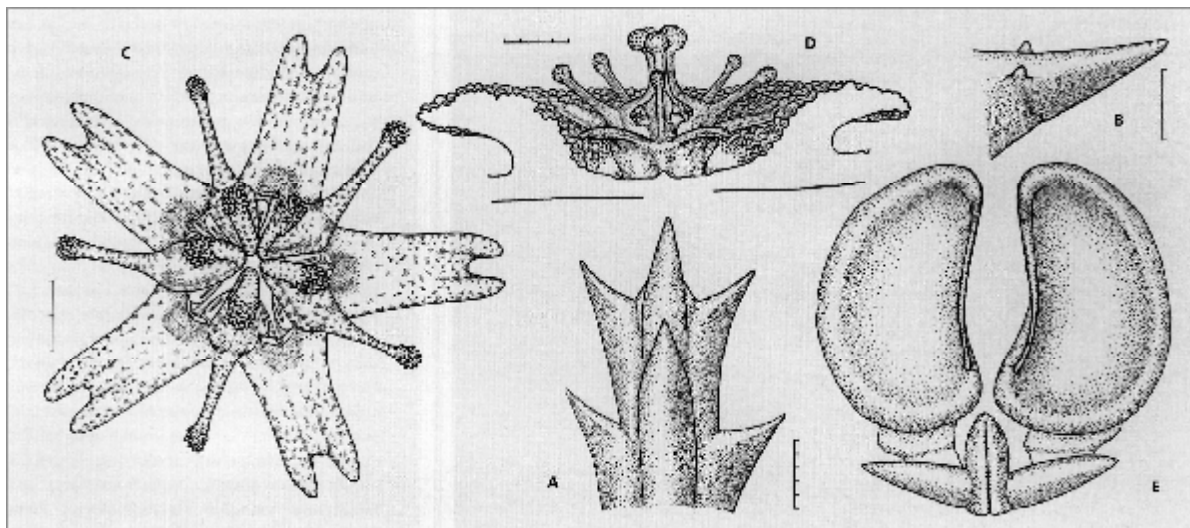


Fig. 10.181. *Orbea variegata*. A, apex of stem. B, apex of tubercle. C, face view of gynostegium. D, side view of centre of dissected flower. E, pollinarium. Scale bars: A, 5 mm; B, 1 mm; C, 2 mm; D, 4 mm; E, 0.25 mm (at B). Drawn from: A, B, D, *PVB 7126*, near Kareedouw; C, *PVB 6261*, Askraal, south-east of Swellendam.

ORBEA VARIEGATA

Orbea planiflora var. *marginata* (Willd.) G.Don, Gen. Hist. 4:120 (1837-8).
Orbea marginata (Willd.) G.Don, Gen. Hist. 4:120 (1837-8).
Stapelia variegata var. *marginata* (Willd.) N.E. Br., Fl. Cap. 4(1):998 (1909).
 Type: Cape of Good Hope (B-W 5303).
Stapelia opbiuncula Haw., Syn. Pl. Succ.: 27 (1812).
 Type: unknown.
Podanthes lepida Haw., Syn. Pl. Succ.: 34 (1812).
 Type: unknown.
Orbea quinquerervia Haw., Syn. Pl. Succ.: 38 (1812).
Stapelia quinquerervia (Haw.) Schult. in Roem. & Schult., Syst. Veg. 6: 37 (1820) as 'S. quinquerervis'.
 Type: unknown.
Orbea bisulca Haw., Syn. Pl. Succ.: 39 (1812).
Stapelia bisulca (Haw.) Schult. in Roem. & Schult., Syst. Veg. 6: 37 (1820).
 Type: unknown.
Orbea bufonia Haw., Syn. Pl. Succ.: 40 (1812).
Stapelia bufonia (Haw.) Sims, Bot. Mag. 40:t.1676 (1814) as 'S. bufonis', non Jacq. (1806-19).
 Type: unknown.
Orbea curtisii Haw., Syn. Pl. Succ.: 40 (1812).
Stapelia curtisii (Haw.) Schult. in Roem. & Schult., Syst. Veg. 6: 38 (1820).
Stapelia variegata var. *curtisii* (Haw.) N.E. Br., Hooker's Icon. Pl. 20: sub t.1907 (1890).
 Lectotype: Bot. Mag. 1: t. 26 (1787).
Orbea anguinea Haw., Syn. Pl. Succ.: 41 (1812).
 Type: unknown.
Orbea retusa Haw., Syn. Pl. Succ.: 41 (1812).
Stapelia retusa (Haw.) Schult. in Roem. & Schult., Syst. Veg. 6: 41 (1820).
Stapelia variegata var. *retusa* (Haw.) N.E. Br., Fl. Cap. 4(1):1003 (1909).
 Type: unknown.
Orbea woodfordiana Haw., Syn. Pl. Succ.: 42 (1812).
Stapelia woodfordiana (Haw.) Schult. in Roem. & Schult., Syst. Veg. 6: 41 (1820).
 Type: unknown.
Stapelia obliqua Willd., Enum. Pl. Suppl.: 13 (1814).
Tromotriche obliqua (Willd.) Sweet, Hort. Brit. ed. 1: 278 (1826).
 Type: material cultivated at the Botanical Garden in Berlin (B-W 5312).
Orbea inodora Haw., Suppl. Pl. Succ.: 12 (1819).
Stapelia inodora (Haw.) Decne., DC, Prodr. 8: 661 (1844).
 Type: unknown.
Stapelia atropurpurea Salm-Dyck, Hort. Dyck.: 372 (1834).
Stapelia variegata var. *atropurpurea* (Salm-Dyck) N.E. Br., Fl. Cap. 4(1):1005 (1909).
 Type: unknown.
Stapelia atrata Tod., Hort. Bot. Panorm. 1: 50 (1877).



Fig. 10.182. *O. variegata*, PVB 6179, Eland's Bay.

Stapelia variegata var. *atrata* (Tod.) N.E. Br., Fl. Cap. 4(1):1006 (1909).
 Lectotype: Hort. Bot. Panorm. 1:t.13, fig. 1.
Stapelia scutellata Tod., Hort. Bot. Panorm. 1: 52 (1877).
 Lectotype: Hort. Bot. Panorm. 1:t.13, fig. 2.
Stapelia horizontalis N.E. Br., Hooker's Icon. Pl. 20: t. 1907 (1890).
Stapelia variegata var. *horizontalis* (N.E. Br.) N.E. Br., Fl. Cap. 4(1):1001 (1909).
 Type: cultivated plants, Barkly 4 (K).
Stapelia variegata var. *pallida* N.E. Br., Hooker's Icon. Pl. 20: sub t.1907 (1890).
 Type: cultivated plants from Port Elizabeth, sub Barkly 2 (K).
Stapelia scylla Sprenger in Cat. Dammann & Co.: 120 (1894).
 Type: unknown.
Stapelia hispida Horn ex Rust, Monatsschr. Kakteenk. 6: 37 (1896).
 Type: unknown.
Stapelia natalensis Rust, Monatsschr. Kakteenk. 6: 37 (1896).
 Type: unknown.
Stapelia variegata var. *prometheus* Dammann ex Rust, Monatsschr. Kakteenk. 6: 37 (1896).
 Type: unknown.
Stapelia ciliolulata Tod. ex Rust, Monatsschr. Kakteenk. 6: 38 (1896).
 Type: unknown.
Stapelia atrata var. *tigrina* Rust, Monatsschr. Kakteenk. 6: 38 (1896).
 Type: unknown.
Stapelia atrata var. *proboscidea* Rust, Monatsschr. Kakteenk. 6: 39 (1896).
 Type: unknown.
Stapelia putida A.Berger, Monatsschr. Kakteenk. 19:159 (1905).
Stapelia variegata var. *picta* f. *putida* (A.Berger) A.Berger, Stap. u. Klein.: 213 (1910).
 Neotype: Berger, Stap. u. Klein.: fig. 47.
Stapelia variegata var. *brevicornis* N.E. Br., Fl. Cap. 4(1):1003 (1909).
 Type: without locality, Chalwin sub N.S. Pillans 47 (BOL).



Fig. 10.183. *O. variegata*, PVB 7126, near Kareedouw.

Stapelia variegata var. *laeta* N.E. Br., Fl. Cap. 4(1):1004 (1909).
 Lectotype: Robben Island, N.S. Pillans 24 (BOL).
Stapelia variegata var. *asparagensis* H.Jacobsen, Sukkulente: 206 (1933).
 Type: unknown.

Small succulent forming clump 50-200 mm (-1 m) diam., not rhizomatous. Stems 25-100 mm long, 5-10 mm thick (excluding teeth), (shortly) decumbent, green mottled with purple-brown; tubercles 3-9 mm long, arranged loosely into 4 obtuse rows along stem with groove between rows, tapering into spreading to ascending conical acute tooth often with minute denticle on either side near apex. Inflorescence 1 per stem near base, of 1-3 flowers developing successively from short peduncle (to $\pm$ 10 mm long), with few small subulate bracts (< 1.5 mm long); pedicel 20-60 mm long, 2-3 mm thick, horizontal usually with ascending apex holding flower facing upwards, pale green to pinkish streaked with red-purple; sepals 5-8 mm long, 2-3 mm broad at base, ovate to ovate-lanceolate, acute to acuminate. Corolla 45-80 mm diam., $\pm$ rotate; outside smooth, pale cream-green becoming veined with red-purple towards tips of lobes; inside rugulose on annulus, transversely rugulose on lobes becoming nearly smooth towards tips as well as base of tube and behind rim of annulus, cream to greenish yellow variously spotted with purple-brown with fewer and finer dots on annulus; tube shallowly bowl-shaped, formed by annulus around gynostegium, annulus pentagonal to circular and 18-23 mm diam., shallowly bowl-shaped with spreading to recurved and thinner rim, with dense ring of short erect cylindrical bristles in base around gynostegium; lobes 16-25 mm long, 12-21 mm broad at base, ovate, acute to shortly acuminate, spreading to slightly recurved, margins eciliate. Corona $\pm$ 8 mm tall, 12-15 mm broad, raised above base of tube on short cylindrical stipe < 1 mm tall; outer lobes 4-6 mm long, 2 mm broad, ascending spreading, linear-oblong narrowing slightly towards 2-3-toothed apex, slightly thicker along centre than towards sides, cream dotted with purple-brown (larger purple-brown patch at base under guide-rail); inner lobes 3-4 mm long, adpressed to backs of anthers then rising up connivent-erect in centre and recurved towards tips, dorsiventrally flattened and ovate near base then narrowing to nearly terete and with clavate-tuberculate apex, with ascending slightly spreading laterally flattened dorsal horn up to 3-4 mm long below level of anthers also with clavate-tuberculate apex, cream dotted with purple-brown.

Distribution and habitat

Orbea variegata is widespread in the south-western Cape, with its northernmost stations around Lambert's Bay and Clanwilliam, where increasing aridity is evidently a limiting factor. From here it is found southwards to the hills around Cape Town and is recorded along the Cape Peninsula to near its southern tip; it is the only stapeliad which occurs on the peninsula. Further eastwards it grows on the coastal plain south of the Langeberg to Riversdale, Mossel Bay, Humansdorp and near Hankey. There are also scattered records from the Karoo around Worcester and in the southern parts of the Great Karoo, e.g. Matjiesfontein (White & Sloane 1937: fig. 673), and specimens from Willowmore and Steytlerville (Leach 1978a). Some of these might well represent escapes from local gardens, in which it is frequently cultivated, rather than records of naturally occurring populations.

Orbea variegata generally grows on gentle (more rarely steep), stony slopes, sometimes under bushes but also more or less fully exposed on rock slabs or ledges. It is particularly common on granitic hillsides from St Helena Bay southwards to the Cape Peninsula, where it grows in large quantities in Camps Bay, on the slopes of Signal Hill, and lower slopes of Lion's Head and around the lower cable station on Table Mountain. Thus, although expansion of the city of Cape Town has undoubtedly contributed to the reduction of its habitat, it almost certainly still grows in reasonable numbers in spots where some of the first European visitors to the Cape of Good Hope must have found it to be plentiful.

Diagnostic features and relationships

The stems of *O. variegata* are fairly slender and are packed, usually densely, into mats which may reach 1 m in diameter or even more. The tubercles vary in prominence but do not bear such long and slender teeth as are found, for example, in *O. longidens*. These teeth become worn down with age, for plants of *O. variegata* seem to become very old in habitat, and in older stems they may be hardly visible at all. When young and somewhat exposed to the sun, the stems are strikingly mottled with purple-brown on green but, in exposed plants, they become uniformly purple-brown with age.

Orbea variegata has fairly large, flat flowers that are pressed to the ground and face upwards. They are extremely variable in colour (and a wide selection of variants was illustrated by White & Sloane (1937)) but usually they are speckled with purple-brown on a pale yellow background. The ovate lobes spread out but are occasionally rolled back behind the flower. The centre of the corolla is more or less flat but near its base there is an additional



Fig. 10.184. *O. variegata*, PVB 7126, near Kareedouw.

ring-like annulus (rather like a double corolla) which rises out of the surface and spreads outwards. While not quite as massive as that in *O. ciliata*, this annulus still manages to form a bowl-shaped tube which contains most of the gynostegium. It is thickest at its base and becomes progressively thinner towards its edge. In the base of this tube around the foot of the gynostegium there is a dense crust of small cylindrical hairs (as in fig. 29 G). Most of the inside of the corolla is covered with raised, finely papillate, irregularly transverse ridges (fig. 29 A) which gradually fade out towards the tips of the lobes. They become especially close together and rough on the annulus but suddenly disappear just above the ring of small hairs near the base of the tube.

The comparatively large gynostegium is raised on a stipe and more or less fills the mouth of the broad annulus. The outer lobes spread widely towards the side of the tube formed by the annulus. They are often shallowly bifid at their apices and are somewhat grooved towards the base beyond the nectarial cavity. The inner lobes are adpressed to the anthers, after which they rise up in the centre in a column with slightly recurved, tuberculate-clavate apices. Each has an ascending-spreading dorsal horn, nearly as large as the lobe itself, and this also has a slightly swollen, tuberculate apex. Most of these lobes are cream spotted with purple-brown, their colour matching fairly closely the colour of the corolla.

Orbea variegata is closely related to *O.*



Fig. 10.185. *O. variegata*, Signal Hill, Cape Town, in habitat, September 1996.

ORBEA LONGII

namaquensis (a fact which is strongly supported by molecular data), which occurs to the north in the much more arid parts of Namaqualand; differences between them are discussed under that species. To the east and partly overlapping with its distribution are the other closely related species, *O. pulchella* and *O. verrucosa*. From both of these *O. variegata* differs by the generally larger flowers with their much more developed annulus and the considerably longer outer and inner corona lobes, with prominent dorsal horns on the inner lobes.

History

The first known record of *O. variegata* was made by Justus Heurnius, who was at that stage of his life a missionary on his way to the Dutch East Indies. The ship on which he was travelling put in for water and fresh meat at Table Bay in April 1624, and while the captain bargained for meat, Heurnius made a little expedition, possibly to the slopes of Table Mountain. There he made drawings of 10 plants, one of which was *O. variegata*. He sent these drawings back to his brother Otto at Leiden, who passed them on to Johannes Bodaeus A Stapel and they were ultimately published, after the early death of Á Stapel, by his father Egbert Bodaeus Á Stapel in Amsterdam in 1644.

Many travelers stopped at Table Bay, where *O. variegata* is also common on the lower slopes of Signal Hill near the coast and on Robben Island in the Bay, so some of them must have taken material of it back to Europe. There is no doubt that it was by a long way the first stapeliad recorded and cultivated in Europe. Already in 1737, Linnaeus established the genus *Stapelia* for it and *S. hirsuta*.

Over its long history, there has been more unjustified and pointless 'splitting' of *O. variegata* than of any other stapeliad (Leach 1978a). Many of the authors of these names have themselves cast doubt as to whether they are distinguishable with any certainty from *O. variegata*. Several people involved themselves deeply in the study of *O. variegata* and its almost innumerable hybrids, and this was particularly the case with David Rust of Hanover in Germany around the close of the 19th century. White & Sloane (1937) managed to construct a key to many of the varieties of *O. variegata*, which was based to a large extent on that of N.E. Brown (1907-09). However, they also pointed out the extent of the variability of the species, how many of these varieties had been found cohabiting within an area of a few square meters and that the same plant even produces rather different flowers on occasion. The complete synonymy of *O. variegata* is given above and it is the most extensive for any stapeliad.

28. *Orbea longii*

Orbea longii (C.A.Lückh.) Bruyns, comb. nov.
Stapelia longii C.A.Lückh., S. African Gard. & Country Life 25: 96 (1935).
Tridentea longii (C.A.Lückh.) L.C. Leach, Trans. Rhod. Scient. Assoc. 59: 4 (1978).
Tromotriche longii (C.A.Lückh.) Bruyns, S. African J. Bot. 61: 204 (1995).
 Type: South Africa, Cape, Paardepoort, F. R. Long sub Lückhoff 220 (missing).
 Neotype: Paardepoort, Leach & Bayliss 15680 (SRGH, holo.; K, PRE, iso.).



Fig. 10.186. *O. longii*, PVB 4928, Sondagrivierpoort.



Fig. 10.187. *O. longii*, PVB 5000, Kabouga, western end of Suurberg.

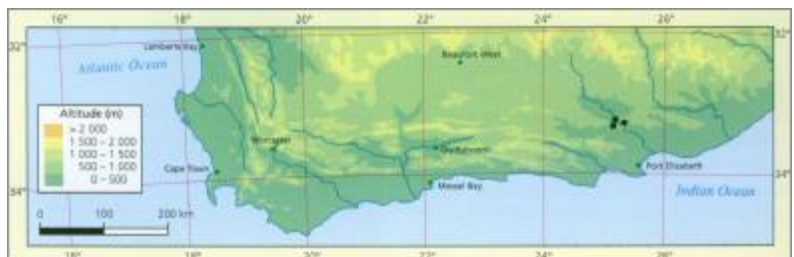


Fig. 10.188. Distribution of *Orbea longii*.

Small succulent spreading to form loose clump or pendent from ledges on cliffs. Stems 40-300 mm long, 4-8 mm thick, prostrate or ascending then soon arching back to ground and sometimes somewhat rhizomatous, pale bluish green mottled with purplish; tubercles 1-2 mm long, joined into 4 obtuse angles along stem, with small spreading to retrorse deltoid tooth towards end nearest apex of stem, tooth somewhat flattened above. Inflorescences 1-2 per stem arising towards apex, bearing 1-2 flowers developing in gradual succession on short peduncle with short deltoid acute bracts 1.0-1.5 mm long; pedicel 10-40 mm long, 1.5 mm thick, ascending and holding flower facing upwards; sepals $\pm$ 3 mm long, 1.5 mm broad at base, lanceolate, acute. Corolla 18-25 mm diam., rotate and somewhat convex above; outside dull green to brown becoming pale behind sepals; inside shiny yellowish to reddish brown usually becoming paler and often finely mottled with (slightly sunken) transverse reddish brown bars on yellow towards annulus, smooth to very faintly transversely rugulose around bases of lobes, without papillae; tube (0.75-) 1.5-2.0 mm deep, pentagonal, shallowly cupular, formed by abrupt annular thickening near base of otherwise $\pm$ flat corolla; lobes 7-9 mm long, 6-8 mm broad at base, mostly slightly reflexed, ovate-deltate, acute, margins somewhat folded back, with vibratile dark purple spatulate-clavate cilia $\pm$ 2 mm long towards base. Corona $\pm$ 4 mm tall, 7-8 mm broad, purple-black, raised on very short stipe; outer lobes 2.5-3.5 mm long, 1.5 mm broad, slightly ascending, rectangular in lower 2 mm and becoming channelled towards base with raised ridges near edges fusing to bases of inner lobes to form shallow pouch under guide-rails, bifid towards apex (sometimes quite

deeply) into obtusely tuberculate spherical knobs; inner lobes 1.5-2.0 mm long, adpressed to backs of anthers then erect, dorsiventrally flattened in lower half then terminating in obtusely tuberculate spherical knob, with very similar (except slightly laterally flattened especially in lower portion) spreading dorsal horn 1.5-2.0 mm long.

Distribution and habitat

Orbea longii is endemic to the Eastern Cape, where it occurs in the Klein Winterhoek Mountains and at the western end of the Suurberg. Plants are always found in steep areas exclusively on soils of sandstone origin. They appear to prefer exposed, well-drained spots usually with only very shallow soil covering rock ledges. The pendent habit observed in Paardepoort by Leach (1980a: fig. 37) has been found only intermittently at the other localities now known and does not seem to be the most typical habit of this species. Even in Paardepoort plants are mainly found creeping in leaf-litter under small bushes on ledges and rock outcrops and this is the habit that has been observed most commonly in the other localities. Specimens are often associated with shrubs of *Crassula rupestris* subsp. *rupestris* and may grow in small accumulations of leaf-litter under these bushlets.

Diagnostic features and relationships

The stems of *O. longii* are always 4-8 mm thick. They are always prostrate and have a distinctive, bluish green hue, becoming grey and faintly mottled with purplish if exposed to the sun. Each tubercle has a quite obvious tooth which is positioned very near the base of the next tubercle above it and has a flattened upper surface. Unusual for a species of *Orbea* is their somewhat papillate surface (Bruyns 1995a), though this is only visible at high magnification.

Flowers are sparsely produced near the apex of the stems on a short peduncle. The comparatively long and fairly slender pedicels hold them well away from the stem, usually facing upwards. The inside of the corolla is an unusual, somewhat shiny reddish brown on the lobes that becomes finely barred with transverse lines towards the centre. It is convex above with the deltate, conspicuously ciliate lobes somewhat reflexed. Towards the centre the corolla has an abrupt, annular thickening (often divided partly into five islands) which gives rise to a small corolla tube in the centre. However, the annulus and the corolla tube are only really conspicuous when the flower is dissected. The



Fig. 10.189. *O. longii*, PVB 8419, near Kabouga, western end of Suurberg.

flowers emit a slight, unpleasant odour.

In the centre of the flower, projecting beyond the mouth of the tube, lies the complicated blackish corona which has a furry-glistening appearance caused by the shiny tuberculate apices of all the lobes of the inner and the outer corona. The outer lobes, which spread out just above the annulus, are each bifid towards the tips into two scarcely divergent lobules, each with a clavate-tuberculate apex. The inner lobes rise in the centre in a small cluster and each also has a clavate-tuberculate apex. Even each spreading dorsal horn on the inner lobes has its own clavate-tuberculate apex. These structures are unique in *Orbea*.

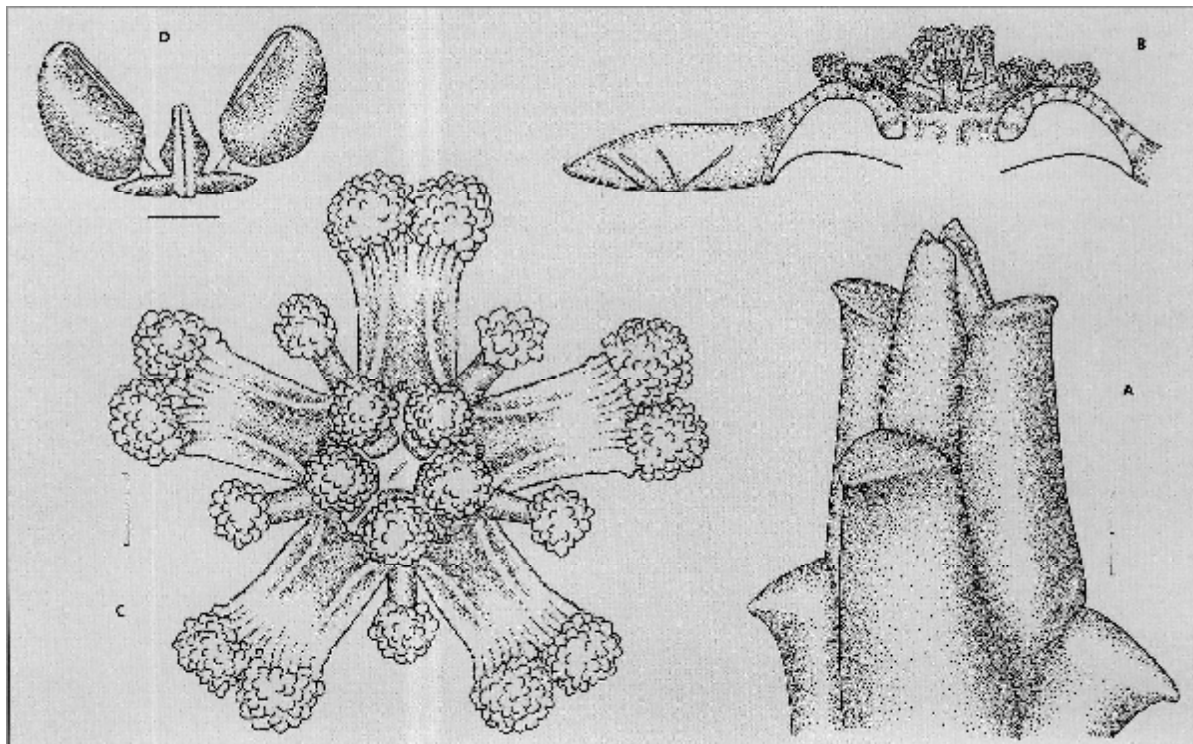


Fig. 10.190. *Orbea longii*. A, apex of stem. B, side view of dissected flower. C, face view of gynostegium. D, pollinarium. Scale bars: A, 2 mm; B, 2 mm (at C); C, 1 mm; D, 0.25 mm. Drawn from: A, B, PVB 4928, Sondagrivierpoort; C, D, PVB 1593, north of Kirkwood.

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Fig. 10.191. *O. longii*, PVB 1593, north of Kirkwood.

History

Orbea longii was first recorded by Frank R. Long in 1934 at Paardepoot, in the Klein Winterhoek Mountains south of Jansenville. Long (1948) told of his discovery this species, which happened entirely fortuitously while scrambling about on some steep slopes trying to reach plants of a *Haworthia*. After clutching at a tuft of grass, which gave way, he fell down the slope. At the end of his fall he found that he still had the tuft in his hand and noticed what looked like a stem of *Ceropegia stapeliiformis* projecting from it. Being a little unsure of the real identity of his find, he grew a piece of it and when it flowered it was revealed to be a new species of *Stapelia*. Long mentioned also that he never saw it again and, until recently, it was known only from this locality (Leach 1980a). Recent exploration in the area by the present author has revealed its presence at several other precipitous places nearby in these mountains and also in gorges at the western end of the Suurberg.

Leach (1978b) placed this species in *Tridentea* and Bruyns (1995a) moved it to *Tromotriche*. Certainly the strange, clavate shape of the corona lobes suggests that it belongs in *Tromotriche*, where such structures are common. However, with their obvious teeth, the stems do not have the rounded and nearly cylindrical appearance that is typical for the species of *Tromotriche*. The outer corona lobes are comparatively large relative to the other lobes, they are bifid towards their tips and are grooved above towards the base. All of these features are unusual within *Tromotriche*. Molecular data show that this species belongs in *Orbea*. Many of its anomalous features in *Tromotriche* fit more comfortably into *Orbea*, where the mottled stems with their obvious teeth are not out of place. The stems are indeed unusually long and slender in *Orbea*, but are not all that different from those in the next two species.

29. *Orbea conjuncta*

Orbea conjuncta (A.C.White & B.Sloane) Bruyns, *Aloe* 37: 74 (2001).

Stultitia conjuncta A.C.White & B.Sloane, *Cact. Succ. J. (US)* 10: 69 (1938).

Orbeanthus conjunctus (A.C.White & B.Sloane) L.C.Leach, *Exceisa Taxon. Ser.* 1: 73 (1978).

Type: South Africa, without locality, comm. Herre (missing).

Neotype: Transvaal, hills above Mara, Crundail (PRE).

Dwarf succulent forming sprawling mat from 100 mm to 2 m diam. or hanging from ledges on rocky outcrops or cliffs, not rhizomatous. Stems 50-200 mm long, 6-10 mm thick (excluding teeth), prostrate, branching all along length, grey-green mottled with dark green to purple; tubercles 2-6 mm long, arranged very loosely into 4 rows along stem with slight groove between rows, tapering into deltoid acute $\pm$ conical spreading tooth, without stipular denticles. Inflorescence 1 (-2) per stem usually towards base, of 1 (-2) flowers developing in gradual succession from very short peduncle (1-2 mm long), with few minute lanceolate bracts (< 1.5 mm long); pedicels 8-14 mm long, 1.5-3.0 mm thick, slightly ascending, holding flower facing partly upwards; sepals 3-5 mm long, 2 mm broad at base, ovate-lanceolate, acuminate. Corolla 20-33 mm long, 22-42 mm broad, bicampanulate; outside smooth, cream suffused with pink; inside maroon to deep pink on lower tube annulus and base of upper tube, rest of tube and lobes cream (base sometimes also maroon); tube 12-18 mm deep, cupular, slightly narrowing towards mouth, at base with further (lower) bowl-shaped tube 5-7 mm long and 10-15 mm broad formed by 2-3 mm thick inward-pointing pentagonal annulus; lobes 6-17 mm long, 9-15 mm broad at base, ascending to spreading, deltate, acute, somewhat concave above, with sutures running from bases a further 5-10 mm down along tube (so that tube partly formed from fusion of lobes and lobes really 11-20 mm long), margins eciliate. Corona 5-7 mm tall, 9-10 mm broad, raised above base of tube on very short stipe (< 1 mm long) usually just included within lower tube; outer lobes 3-6 mm long, ascending with spreading apices,

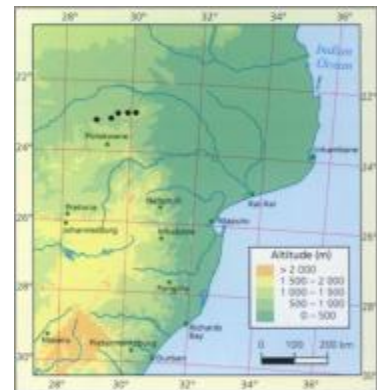


Fig. 10.192. Distribution of *Orbea conjuncta*.

deeply bifid (often to near base) into widely diverging lanceolate obtuse dorsiventrally-flattened lobules, lobules from adjacent lobes usually adpressed to one another, deep pink to maroon speckled with white towards base, papillate-pubescent towards apices, covered with droplets of sweat-like secretion around gynostegium above base of inner lobes; inner lobes $\pm$ 1 mm long, adpressed to backs of anthers and sometimes exceeding them (to meet and rise up slightly in centre), dorsiventrally slightly flattened with small obtuse basal dorsal gibbosity connected to outer series, deep pink to maroon spotted with white, finely papillate especially towards apices.

Distribution and habitat

Orbea conjuncta is widely distributed and quite common in the Soutpansberg from near Vivo in the west to Nzhelele, some 30 km east of Wyllie's Poort, and it might well occur still further east. It was thought to be endemic to the Soutpansberg. However, my own investigations revealed that it also grows in the Blouberg, a similar range of mountains slightly to the west of the Soutpansberg and it was recorded there



Fig. 10.193. *O. conjuncta*, PVB 6570, western end of Soutpansberg, near Vivo.



Fig. 10.194. *O. conjuncta*, PVB 6990, Blouberg near Buffelshoek.

for the first time in January 1997.

Although plants have repeatedly been collected 'on ledges on steep rock cliffs' (Leach 1978a) in Wyllie's Poort, the type locality, this is mainly because of the proximity of this spot to the road and it seems that *O. conjuncta* has now been more or less eradicated there as a result of collecting. A few plants have been seen hanging from ledges on similar cliffs along the steep sides of a riverbed west of Mara. Nevertheless,

it appears that such habitats have little to do with the real preference of this species. *Orbea conjuncta* is mostly found on the southern aspects of mountains, usually relatively high up on gentle to steep slopes, among leaf-litter under bushes or trees. In many localities in the Soutpansberg (particularly east of Soutpan) it is associated with forests of the euphorbiaceous tree *Androstachys johnsonii* (the Lebombo ironwood), which forms characteristically

dense and dark green thickets on stony slopes on the mountains. Plants of *O. conjuncta* form prostrate mats among the dead leaves and twigs between rocks and the stems of these trees on the floor of such a 'forest'. These 'forests' harbour practically nothing else as undergrowth. Despite their apparent denseness, such ironwood thickets are not particularly shady and the stems of *O. conjuncta* are often to some extent exposed and may then be prettily mottled with purple on grey-green.

Diagnostic features and relationships

The stems of *O. conjuncta* are prostrate (rarely pendulous) and root wherever they touch the soil, branching also randomly along most of their length. They form fairly diffuse mats which may spread for up to 1 sq m or more. The tubercles are well spaced out along the stem and have relatively short, conical teeth on them. They are loosely arranged into four obtuse rows along the stems, with a slight groove between these rows.

Florally this must surely rank as one of the most remarkable of the stapeliads. The whole exterior of the flower is cream, faintly suffused with pink. Much of the inside is also this colour but this changes abruptly below the middle to a deep pink or maroon, sometimes becoming cream again behind the corona.

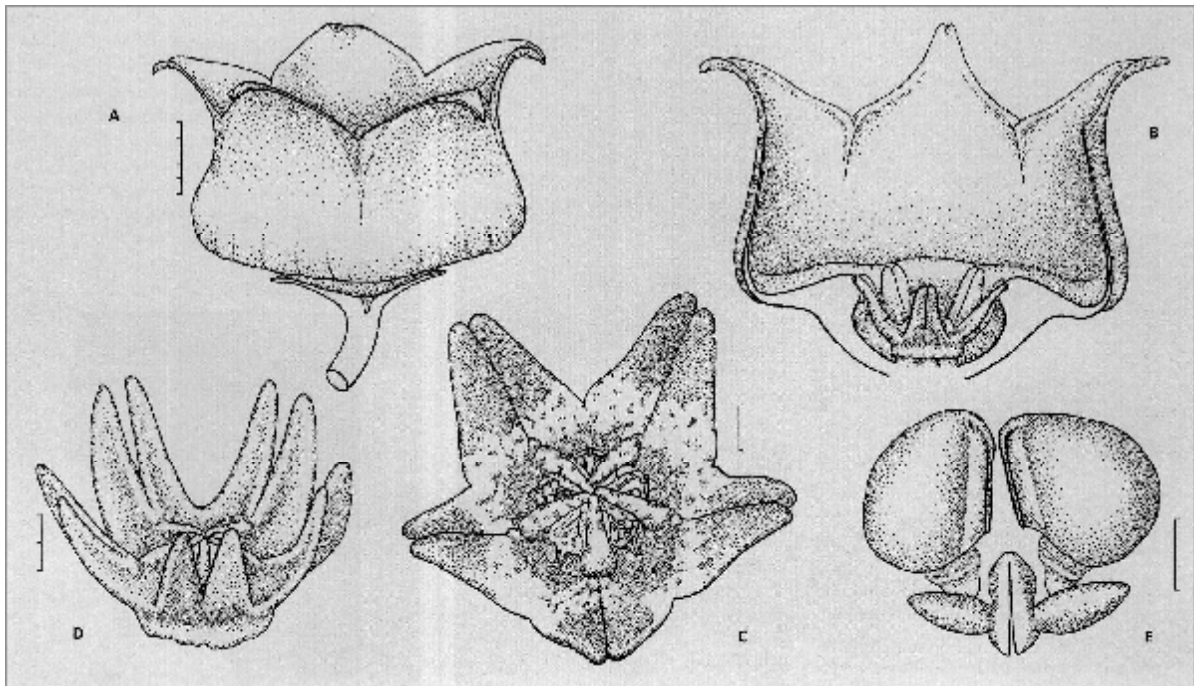


Fig. 10.195. *Orbea conjuncta*. A, side view of flower. B, side view of dissected flower. C, face view of gynostegium. D, side view of gynostegium. E, pollinarium. Scale bars: A, B, 5 mm (at A); C, 1 mm; D, 2 mm; E, 0.25 mm. Drawn from A, C, E, PVB 4477, west of Wyllie's Poort, Soutpansberg; B, D, PVB 6570, western end of Soutpansberg, near Vivo.



Fig. 10.196. *O. conjuncta*, PVB 7467, Soutpansberg near Nzehele Dam, with 'furry' corona clearly visible.

The flowers emit a faint odour of excrement when they are newly open. However, it is the shape of the flower that is particularly unusual. The base consists of a bell-shaped cup whose mouth is greatly constricted on the inside by a thick, inward-pointing annulus. Beyond this annulus the tube is abruptly much broader but narrows again towards the mouth, from which the deltoid lobes (which are noticeably concave inside) spread outwards, often only slightly. The corolla is therefore referred to as bicanalulate, i.e. consisting of a double bell. However, it is also noteworthy that the upper bell is not part of the true corolla tube, which lies below the annulus, but is formed by partial fusion of the corolla lobes.

In young buds (say, 10 mm long) the lobes occupy 7 mm (i.e. most) of the length of the flower, with clear sutures visible along the exterior where they are fused. However, when the flower ultimately opens the lobes occupy much less than half the length of the corolla. This is not due to changes in the rates of growth of the different parts but by the lobes remaining fused towards their bases so that this fused part adds to the length of the tube. In the mature flower traces of this fusion are still visible on the inside as a raised ridge and on the outside as a groove, as White & Sloane (1938) pointed out.

The comparatively large corona is seated in the lower tube, with the outer lobes ascending steeply and pressed against the inner rim of the annulus. These outer lobes are deeply bifid, with the lobules that this produces diverging widely so that those from adjacent lobes are paired behind the anthers and create the appearance of outer lobes opposite the anthers. The outer lobes are deep pink to maroon towards the tips (matching the colour of the annulus), becoming paler and speckled with white towards the middle and sometimes

becoming dark again at the base. The inner lobes are small and adpressed to the backs of the anthers. Both series of corona lobes are covered with fine transparent papillae which lend them a furry appearance. There are usually several large drops of nectar secreted on the outer lobes just above where they are fused to the inner lobes.

Despite the obvious differences between their respective flowers (see under *O. hardyi*), *O. conjuncta* and *O. hardyi* are obviously closely related and this is strongly supported in our molecular analyses. Meve & Liede (2002) found that the relationship of *O. hardyi* (the only one of the two that they included) to *Orbea* was unresolved, but despite this, they concluded that they belonged to separate genera. Our own analyses place both of them within *Orbea* and consequently they are both kept within *Orbea* here.

History

This strange stapeliad was discovered by the intrepid walker and Barclays Bank official Albert Henry Crundail in the hills west of Mara (west of Louis Trichardt) a little before 1938. Material from his collection was sent by Hans Herre to White & Sloane in California and they described it in 1938. No further collections seem to have been made until Roy D.A. Bayliss located it in 1961 on cliffs above the riverbed near the tunnels on the main road through Wyllie's Poort. According to Leach (1978a), Crundall's collection was the only one ever made near Mara, and the species was otherwise known only from several gatherings from the same spot in Wyllie's Poort. Exploration since 1996 by the present author has revealed it to be considerably more widespread and also quite plentiful near Mara.

30. *Orbea hardyi*

Orbea hardyi (R.A.Dyer) Bruyns, *Aloe* 37: 74 (2000).
Stultitia hardyi R.A.Dyer, *Fl. Pl. Africa* 36:t.1403 (1963).

Orbeanthus hardyi (R.A.Dyer) L.C.Leach, *Excelsa* Taxon. Ser. 1:74 (1978).

Type: South Africa, Transvaal, 'Wyllie's Poort', Hardy et al. sub PRE 29028 (PRE).

Dwarf succulent forming sprawling mat from 100 mm to 1 m diam. or more, not rhizomatous. Stems 30-150 (-300) mm long, 6-12 mm thick, slender, prostrate, branching all along length (branches breaking off extremely easily), green with longitudinal purple-brown stripes and blotches; tubercles 1-3 mm long (nearly obsolete) and stems $\pm$ square-cylindrical in cross-section when turgid, arranged very roughly into 4 rounded angles without groove between angles, tapering abruptly into short conical tooth without stipular denticles. Inflorescence 1 (-2) per stem usually towards base, of 1-2 flowers opening in gradual succession from very short peduncle (1-2 mm long), with few minute lanceolate bracts (< 1 mm long); pedicels 5-8 mm long, 1.5-2.0 mm thick, ascending, holding flower $\pm$ facing upwards; sepals 2.5-6.0 mm long, 1.5 mm broad at base, ovate-lanceolate, acuminate. Corolla 40-75 mm diam., rotate to very shallowly bicanalulate, with united portion shallowly plate-like to abruptly bowl-shaped (up to 8 mm deep below lobes); outside smooth, cream suffused with purplish; inside with clavate maroon to white papillae up to 1-2 mm long on lower half of lobes and 3-5 mm of united area below lobes, otherwise smooth, purple-red to maroon on lobes becoming coarsely mottled with cream towards their bases, purple-red to brighter red and more finely spotted with cream on annulus, cream in tube; tube $\pm$ 3 mm long, 15-25 mm broad, very shallowly cupular to nearly flat, with further tubelet around gynostegium 2-3 mm long and 6-8 mm broad formed by circular annulus with $\pm$ 2 mm thick inward-pointing edge; lobes 13-25 mm long, 11-20 mm broad at base, spreading to recurved, ovate, acuminate, flat to very slightly concave above, with sutures running from bases a further 2-3 mm down tube, margins ciliate. Corona $\pm$ 7 mm tall, 8-9 mm broad, raised above base of tube on short pentagonal stipe $\pm$

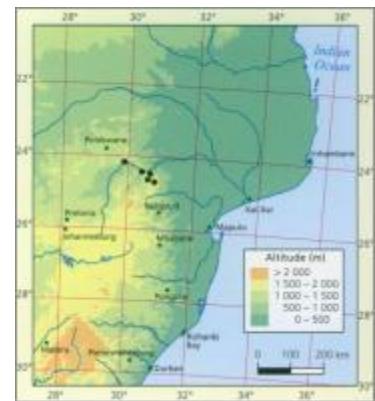


Fig. 10.197. Distribution of *Orbea hardyi*.

1 mm tall; outer lobes 2-3 mm long, ascending then spreading just beyond mouth of tube or adpressed to annulus just outside tube, dorsiventrally flattened, bifid to near base into somewhat divergent obtuse lobules, cream spotted with purple-red, with purple-red margins, papillate-pubescent towards apices; inner lobes 4-5 mm long, adpressed to backs of anthers then connivent-erect and diverging towards slightly clavate apices, cream dotted with purple-red, papillate-pubescent especially towards maroon apices.

Distribution and habitat

Orbea hardyi is not a rare species in the much-dissected and mountainous area of the north-eastern escarpment of South Africa to the south-east of Pietersburg (Polokwane). Here it occurs from Bewaarskloof eastwards along the Olifants River to the Abel Erasmus Pass and southwards along the western edge of the Blyde River Canyon to around the settlement of Moremala.

It may grow on the floor of dry forest on south-facing slopes in accumulated leaf-litter.

Plants also occur on cliffs and rock outcrops where, on exposed slopes, they have even been seen wedged tightly into crevices (as in fig. 10.199), with *Selaginella* and various other succulents (including *Huernia zebrina*).

Diagnostic features and relationships

The stems of *O. hardyi* are similar to those of *O. conjuncta* in habit and are prostrate, forming mats of up to 1 sq m or more. They are often a little thicker, though, and are more round when

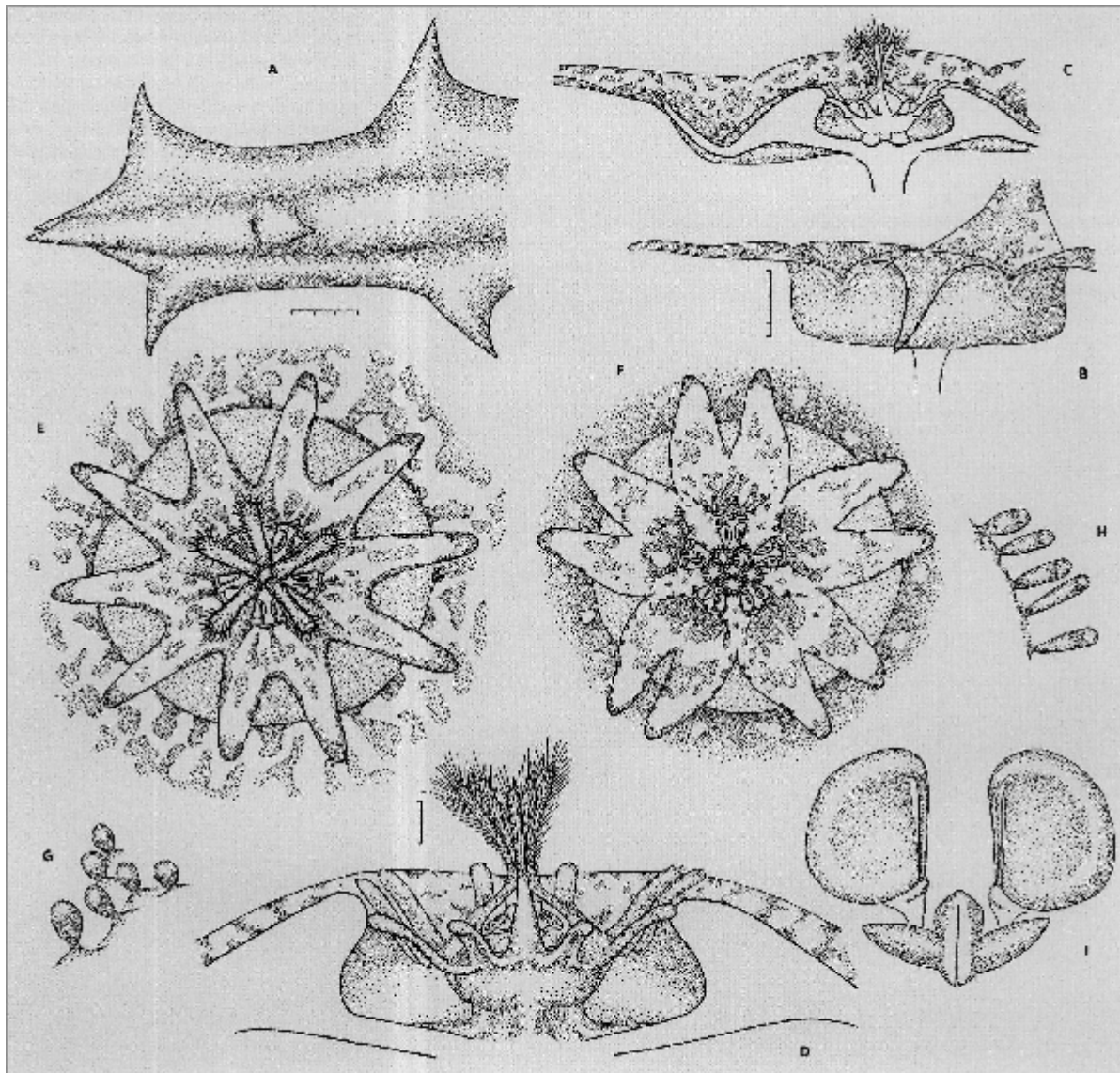


Fig. 10.198. *Orbea hardyi*. A, apex of stem. B, side view of somewhat cupular flower. C, side view of dissected flower. D, side view of centre of dissected flower. E, F, face view of gynostegium. G, H, papillae at base of lobes inside corolla. I, pollinarium. Scale bars: A, 3 mm; B, C, 5 mm (at B); D-F, 1 mm (at D); G, H, 0.5 mm (at A); I, 0.25 mm (at A). Drawn from: A, F, H, PVB 2039, Penge; B-D, I, PVB 7020, near Blyde River Canyon; E, PVB 2030, Abel Erasmus Pass; G, PVB 6606, Branddraai.

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turgid (consequently less square in cross-section) and with less of a groove between the angles. They are often also a little darker with darker mottling. The branches are quite a bit more flimsily attached to older stems than in *O. conjuncta* and often break off at their base at the slightest disturbance.

Flowers in *O. hardyi* are comparatively large (up to 75 mm in diameter) and are almost flat to shallowly bowl-shaped when fully open. The lobes, which are broad at the base and taper into slender tips, spread out as far as the surrounding stems will allow. Inside they are coarsely mottled with maroon on cream, sometimes becoming plain maroon towards the tips. The centre of the flower is dominated by a somewhat raised, cushion-like annulus which is more intensely coloured than the rest of the corolla. This is sometimes almost plain dull maroon but it may also have a much finer mottling of maroon to pink on cream. The annulus lies inside a broad and very shallow tube (the corolla is sometimes nearly wholly flat) so the annulus (as in *O. conjuncta*) forms another tube around the gynostegium and actually the flowers here are also bicampanulate (though very shallowly so). If the flower is dissected (fig. 10.198 C, D) it becomes clear how the edges of the annulus

project inwards towards the centre and create a distinct narrowing in the mouth of this tube. On the lower half of the lobes the inside is quite densely covered with little swollen papillae and these extend onto the often steep, united area below them but not onto the annulus at all. These papillae are extremely variable in shape, ranging from more or less spherical to clavate or cylindrical, but they always have a slender base. They are usually maroon both on the dark patches of the corolla and on the cream areas, but occasionally they are also cream near the edges of the lobes.

As in *O. conjuncta*, part of the tube is formed by the lobes remaining fused near their bases at anthesis. However, in *O. hardyi* this zone of fusion is very much shorter than in *O. conjuncta* and may be quite indistinct.

The bulk of the gynostegium is contained within the corolla tube. The corona is similarly coloured to the corolla except that the lobes are all purple-red or darkly barred along their margins. The outer lobes are deeply bifid with the lobules spreading and often adpressed to the surface of the annulus around the mouth of the tube. The inner lobes are much longer than the anthers, rising in a column quite high above them, and have dark maroon, diverging and slightly swollen tips. Many of the epider-

mal cells of the corona have outer walls that are elongated into slender papillae, lending it a pubescent appearance: these papillae are fine and not easily visible on the outer lobes, where they are mainly confined to the margins and tips. However, towards the tips of the inner lobes these 'hairs' become clearly visible to the naked eye as they are denser and considerably longer. These long inner lobes contrast strongly with the very short ones in *O. conjuncta*.

History

The type of this species was originally said to have been collected by Hardy, Rauh and Bayliss (sub *PRE 29028*) in Wyllie's Poort in the Soutpansberg where it grew intermingled with *O. conjuncta* (Dyer1963). However, it has never been found anywhere near there again. The type sheet has been annotated (dated August 1974) by R.A. Dyer as follows: 'this [locality] is in error: plant was collected in the first place by J.H. van der Merwe between Ohrigstad and Lydenburg at Kasper's Nek'. It can therefore safely be assumed that the type collection was from the 'eastern Transvaal' and not from Wyllie's Poort in the Soutpansberg. The original collection was made in 1958 or 1959 by Johannes H. van der Merwe, who went up



Fig. 10.199. *O. hardyi*, PVB 7020, near Blyde River Canyon, in crevices in dolomite outcrop, January 1997.



Fig. 10.200. *O. hardyi*, PVB 7020, near Blyde River Canyon.

a slope in Kasper's Nek to collect an *Aloe*. On arriving back at the car, some unusual stapeliad stems were noticed among the roots of the *Aloe* that had been brought back. These stems were cultivated and a few were given to D.S. Hardy, who had commented that they seemed most unusual and had asked to be given some (Van der Merwe, pers. comm. 2000). It appears that some horticultural confusion at a later stage resulted in the type locality being given as Wyllie's Poort and in the discovery being credited finally to Hardy.



Fig. 10.201. *O. hardyi*, PVB 7020, near Blyde River Canyon.



Fig. 10.202. *O. hardyi*, PVB 7020, near Blyde River Canyon.